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VERTEBRATE PALEONTOLOGY

*A Redescription of Gymnotrachelus (Placodermi: Arthrodira)
from the Cleveland Shale (Famennian) of Northern Ohio, U.S.A.*

Robert K. Carr

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A REDESCRIPTION OF *GYMNOTRACHELUS* (PLACODERMI: ARTHRODIRA) FROM THE CLEVELAND SHALE (FAMENNIAN) OF NORTHERN OHIO, U.S.A.

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ABSTRACT

The relationships among selenosteoid arthrodires are inadequately known. The recovery of new material for *Gymnotrachelus hydei* Dunkle and Bungart from the Cleveland Shale (Famennian) of northern Ohio, U.S.A., offers a unique insight into an important, but poorly known member of this group. Previous analyses of selenosteoids have suggested that *Gymnotrachelus* represents either a basal member of the Selenosteidae or a taxon of unresolved affinities. The various studies have differed also in the taxa included within the family. The current redescription of *Gymnotrachelus* provides the foundation for a parsimony based cladistic analysis of Selenosteidae using multiple outgroups. In contrast to previous analyses, *Gymnotrachelus hydei* is a derived member of Selenosteidae, sister taxon to *Melanosteus* Lelièvre, Feist, Goujet, and Blicek. *Gymnotrachelus hydei* is characterized by: (1) distinct sensory line grooves bounded by a pronounced lip; (2) a rostral expansion of the preorbital plate over the rhinocapsular region; (3) a pineal plate overlapped by preorbital and central plates; (4) the presence of a gap between submarginal, suborbital, and postsuborbital plates and head shield; (5) anterior superognathals with two posterolateral longitudinal rows of denticles with each row possessing one to three denticles; (6) an inferognathal possessing a single row of denticles with one or two accessory rows posterolaterally; (7) an ovate leaf-shaped parasphenoid with a short stem-like prehypophysial region; (8) an anterior median ventral plate in the form of an isosceles triangle with equivalent length and width; (9) an anterior ventrolateral plate similar in shape to the posterior ventrolateral plate of *Heintzichthys gouldii* (a rounded scalene triangle with the base facing medially); and (10) overlap of the left posterior ventrolateral plate onto the right. *Braunosteus* Stensjö is considered here to be a member of Selenosteidae although further analysis is needed to confirm this relationship.

Introduction

The current description of *Gymnotrachelus hydei* is part of a continuing study of poorly known and undescribed specimens recovered from the Cleveland Shale (Famennian) of northern Ohio, U.S.A. *Gymnotrachelus hydei* was first described by Dunkle and Bungart (1939) based on a single incomplete specimen, preserved in part and counterpart, which had undergone some weathering with further loss of information. Dunkle and Bungart recognized a relationship between *Gymnotrachelus hydei* and selenosteoid arthrodires; however, they did not provide a clear phylogenetic diagnosis. In 1965-1966, The Cleveland Museum of Natural History collected additional *Gymnotrachelus hydei* material during the Interstate 71 Paleontological Salvage Project. I here redescribe *Gymnotrachelus hydei* based on this new material, providing both an update of Dunkle and Bungart's description of *Gymnotrachelus hydei* and a new diagnosis. Finally, I review the phylogenetic relationships of *Gymnotrachelus* to other Selenosteidae, although the relationship of selenosteids to other aspinothoracid arthrodires remains unclear.

A number of workers have evaluated relationships among aspinothoracid arthrodires (Gross, 1932; Stensjö, 1963, 1969; Dunkle and Bungart, 1939; Obruchev, 1964; Denison, 1975, 1978; Lelièvre et al., 1987; Miles and Dennis, 1979; Gardiner, 1990; Gardiner and Miles, 1990; Carr, 1991). Early analyses often lacked phylogenetically informative diagnoses for taxa because of poor preservation and at the time a lack of separation between primitive and derived features. The primary sources for information on aspinothoracid arthrodires are based on materials from two localities: the upper Frasnian Kellwasserkalk of the *Manticoceras* Beds, Germany, and the upper Famennian Cleveland Shale, Ohio, U.S.A. During the Interstate 71 Paleontological Salvage Project (1965-1966) numerous specimens of new or poorly known taxa were recovered. Carr (1991; see also Denison, 1978; Lelièvre et al., 1987) noted insufficiencies in previous analyses of North American and European aspinothoracid arthrodires and provided a limited phylogenetic analysis based in part on undescribed material from The Cleveland Museum of Natural History. The current study of *Gymnotrachelus hydei* provides new data on a poorly known North American taxon that is important for more detailed analyses.

Anatomical abbreviations used in figures and listed at the end of the paper follow those of Dennis-Bryan (1987) and Carr (1991). Specimen number prefixes denote their respective institutions: CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; PM, Peabody Museum, Yale University. The suffix "id" when used to form taxonomic adjectives does not refer to the familial level in Linnean classification, but is used as a convenience for discussing informal taxonomic units.

Methods

Phylogenetic hypotheses are based, in this discussion, on analyses using PAUP (v. 3.1, Swofford, 1993) and MacClade (v. 3, Maddison and Maddison, 1992). Parameters specified in PAUP include the exhaustive search option with all characters unordered and Trematosteidae and Brachydeiridae set as outgroups. The most parsimonious trees (minimal character transformations) are retained for the current discussion.

Systematic Paleontology

- Placodermi McCoy, 1848
- Arthrodira Woodward, 1891
- Brachythoraci Gross, 1932
- Eubrachythoracei Miles, 1971
- Pachyosteina Denison, 1978
- Aspinothoracidi Stensjö, 1959 (*sensu* Miles and Dennis, 1979)
- Selenosteidae Dean, 1901
- Gymnotrachelus* Dunkle and Bungart, 1939

Diagnosis

Gymnotrachelus is a typical aspinothoracid arthrodire characterized by reduction of the lateral and occipital thickenings of the head shield and loss of the spinal plate. The genus is characterized by: (1) distinct sensory line grooves bounded by a pronounced lip; (2) rostral expansion of the preorbital plate over the rhinocapsular region; (3) a pineal plate overlapped by preorbital and central plates; (4) the presence of a gap between submarginal, suborbital, and postsuborbital plates and head shield; (5) anterior superognathals with two posterolateral longitudinal rows of denticles with each row possessing one to three denticles; (6) an inferognathal possessing a single row of denticles with one or two accessory rows posterolaterally; (7) an ovate leaf-shaped parasphenoid with a short stem-like prehypophyseal region; (8) an anterior median ventral plate in the form of an isosceles triangle with equivalent length and width; (9) an anterior ventrolateral plate similar in shape to the posterior ventrolateral plate of *Heintzichthys gouldii* (a rounded scalene triangle with the base facing medially); and (10) overlap of the left posterior ventrolateral plate onto the right.

Type species

Gymnotrachelus hydei Dunkle and Bungart, 1939

Diagnosis

Same as genus.

Holotype

CMNH 5724. Figure 1 depicts a redrawing of Dunkle and Bungart's (1939) camera lucida drawing of the holotype corrected to reflect current plate interpretations.

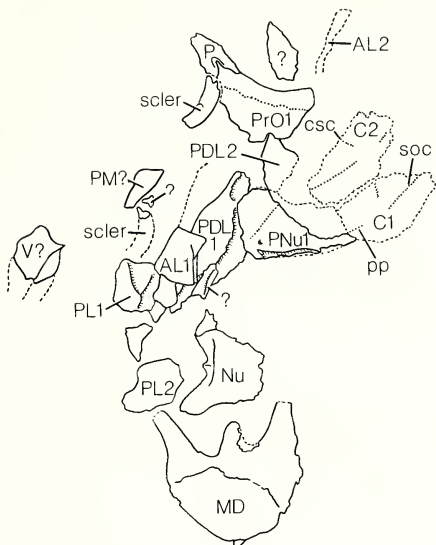


Figure 1. *Gymnotrachelus hydei*. A reinterpretation of Dunkle and Bungart's (1939, fig.1) camera lucida drawing of the holotype CMNH 5724. Structures and archaic terminology are updated based on the current analysis. A numerical postscript of 1 = left and 2 = right.

Additional Material

PM 55665, articulated anterior part of head shield in internal view, isolated suborbital, and inferognathal impression (Figure 3); CMNH 8049, disarticulated thoracic shield, in part, with scapulocoracoid, cheek with sclerotics, and gnathals; CMNH 8050, nearly complete head and thoracic shields in internal view with cheek (including sclerotics) and gnathal plates (Figures 8E, 12B & C); CMNH 8051, disarticulated posterior head shield, cheek with sclerotics, incomplete thoracic shield, and inferognathal (Figures 4B & C, 5, 6, 7B, 8A & B, 11); CMNH 8052, incomplete disarticulated head and thoracic shields, sclerotics, parasphenoid (Figures 4A, 4D & E, 9B, 10); CMNH 8053, gnathals, isolated fragments of head and thoracic shields and cheek (Figures 4F, 9A); CMNH 8054, incomplete, but partially articulated head shield, disarticulated and incomplete cheek with sclerotics and thoracic shield, and inferognathals (Figure 12A & D); CMNH 8055, incomplete cheek with sclerotics, gnathals, one plate and fragment from thoracic shield (Figures 7A, 8D); CMNH 8084, incomplete right inferognathal (posterior occlusal region and blade); CMNH 8776, incomplete

left inferognathal (Figure 8C); CMNH 8778, 8779, and 8788, isolated left posterior superognathals; CMNH 8798, incomplete left suborbital plate; and CMNH 8799, incomplete disarticulated head and thoracic shields, cheek with sclerotics, and fragmented scapulocoracoids.

Occurrence

All material was found within the Cleveland Shale Member (Famennian) of the Ohio Shale, northern Ohio, U.S.A. The holotype was found on Townes Creek, Lorain County, Ohio. Interstate 71 material was recovered from the *Heintzichthys* zone (Carr, 1991) which was quarried at the intersection of West 130th Street and Interstate 71, Cleveland, Ohio. PM 55665 is recorded only as being found in the Cleveland Shale.

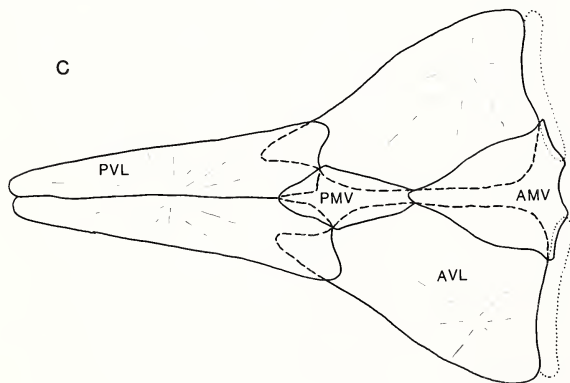
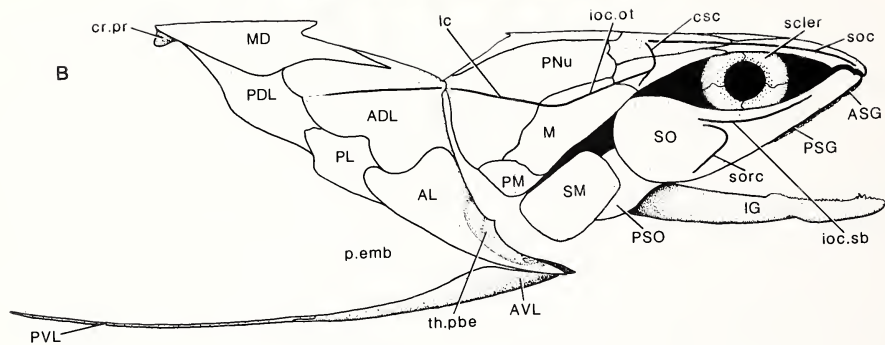
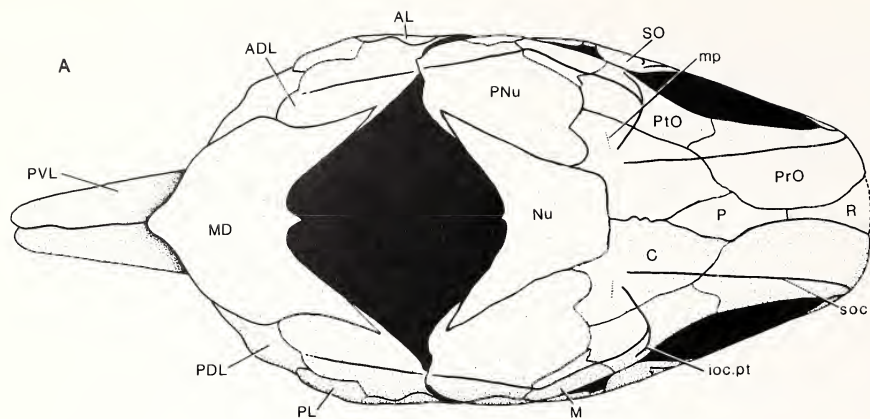
Description

Head Shield

General features. The head shield is composed of 15 plates (Figure 2A & B). Of these, six are paired with three unpaired median plates. There is no evidence for the presence of postnasal or internasal plates. Grooves for sensory lines are present and follow the typical arthrodiran pattern; however, they are bounded by a well-developed lip or ridge. Although ridge prominence is variable within an individual, this character is found consistently within all specimens. This condition is distinctive for *Gymnotrachelus* among aspinothoracid arthrodirans within the Cleveland Shale fauna and is apparently not a simple consequence of bone compression during preservation. All plates are flattened, making interpretations of original curvature difficult.

Rostral (R). A definitive rostral plate is not recognized in any of the specimens. On the basis of the size and shape for the gap between preorbital plates, the rostral plate if present appears to have been triangular in shape with a broad anterior margin (Figures 2A, 3). The presence of a rostral plate is speculative since there is no evidence for either the plate or overlap areas on adjacent plates.

Pineal (P). The pineal plate (Figure 2A) is exposed ventrally in the type (CMNH 5724, Figure 1) and PM 55665 (Figure 3) and exposed externally in CMNH 8052 (Figure 4A) as an isolated plate. The latter specimen has bilateral overlap areas for the central plates (oa.C, Figure 4A) and reduced overlap areas for the preorbital plates (oa.PrO, Figure 4A). In contrast, in *Heintzichthys gouldii* the pineal overlaps both preorbital and central plates while in *Dunkleosteus terrelli* the pineal overlaps central and rostral plates, but is overlain by the preorbital. A central anterior extension of the pineal plate suggests that this plate may have contacted the rostral. This central extension is much narrower than that suggested by Dunkle and Bungart (1939, p. 17). No external overlap



area for the rostral plate is discernible and internally exposed pineal plates do not reveal the anterior region, preventing evaluation for the presence of a rostral contact face. Internally the pineal fossa is bounded posteriorly by a well-developed ridge. A pineal foramen is present externally (Figure 4A).

Nuchal (Nu). The nuchal (Figures 2A & B; 4B & C) is embayed posteriorly with a small process in the midline (p.pr. Figure 4C). In CMNH 8050, the median process is elongate, extending *ca.* 8 mm beyond the posterior margin of the head shield. Long slender alae extend posterolaterally along the nuchal gap. The anterior border of the nuchal is transverse.

The internal nuchal thickening (n.th, Figure 4B) is reduced and limited to the central region. The thickening continues as thin ridges forming the descending faces of the posterolateral alae. Paired pits (pt.u, Figure 4B) open posteriorly and are separated by a median septum (m.sept, Figure 4C) which is continuous with the posterior median process. Distinct muscle pits are absent (f.lv, Goujet, 1984) with muscle insertion limited to two laterally extended shelves or elongate fossae (fe.lv, Figure 4C).

Preorbital (PrO). The preorbital plate (Figures 2A & B; 3) possesses a preorbital process, although it is not pronounced laterally due to the large orbit and gentle curvature of the dorsal orbit border (contrast this with *Dmkleostens* where distinct pre- and postorbital processes denote a smaller orbit with a pronounced curvature). A groove for the supraorbital sensory line traverses the plate and ends near the anterolateral corner (soc, Figures 2A & B). The ratio of longitudinal lengths of the preorbital and central plates is *ca.* 1.1 (PrO/C); the ratio of lengths of the preorbital and postorbital plates is *ca.* 1.2 (PrO/PtO).

Internally, a supraorbital vault (suo.v, Figure 3) is present extending from the preorbital process onto the postorbital plate. Medially, the supraorbital vault shows a recess for the neurocranial preorbital process (ch.pr, Figure 3). Anterior to this recess, a supraethmoid crista is present, but forms a low platform versus a distinct ridge.

Figure 2. *Gymnotrachelus hydei*. Composite reconstructions of head and thoracic shields in A, dorsal view and B, lateral view. Only a few head shield plates are complete in all dimensions; therefore, plate boundaries are reconstructed based on known plate components and potential boundaries and plate overlaps with adjacent plates. The posterior margin of the central and anterior dorsolateral plates are incompletely known. C, a reconstruction of the ventral thoracic plates in dorsal view (no attempt has been made to interpret original curvature). Estimated boundaries for the interolateral plates are drawn in dotted lines. Hidden plate boundaries are drawn in dashed lines.

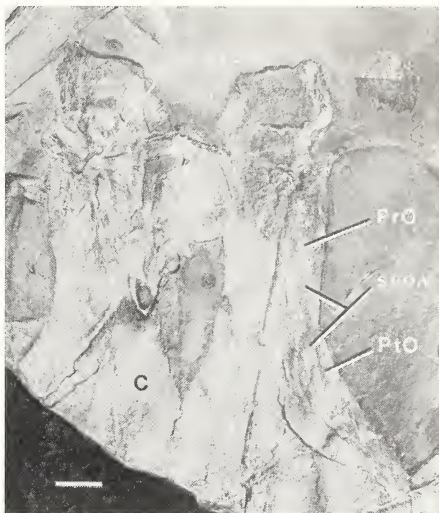


Figure 3. *Gymnotrachelus hydei*. Internal view of an incomplete head shield (PM 55665). Scale bar equals 1 cm.

This platform is confined to the preorbital plate and does not extend medially as does the crista in some European stenolestoids (e.g., *Enseostens*, Stensiö, 1963, fig. 113A). The preorbital plate is expanded anteriorly over the rhinocapsular region (Figure 3; also seen in *Heintzichthys gouldii*, but to a lesser degree, Carr, 1991, fig. 3A; a similar region is seen in tubular snouted coccosteomorphs *Rolfosteus* and *Tubonasis*, Dennis and Miles, 1979). Due to flattening in preservation, it is not clear whether this expansion is downturned in life. Along the plate's lateral margin, there is a shallow notch between the preorbital dermal process and the anterolateral extension over the rhinocapsular region. The supraorbital sensory line groove is detected internally as a raised ridge on the preorbital plate (Figure 3).

Postorbital (PtO). The postorbital plate (Figures 2A & B, 3, 4D) lacks a postorbital process. Grooves for three sensory lines are present on the postorbital plate; central sensory line (csc, Figure 4D) and postorbital and otic branches of the infraorbital sensory line (ioc.pt and ioc.ot respectively, Figure 4D). The central sensory line and the otic branch of the infraorbital line are generally continuous, forming an angle of *ca.* 95°, although they are disjunct on the right postorbital plate in CMNH 8052 (conjoined on the left). The postorbital branch of the infraorbital line does not always unite with the former two sen-

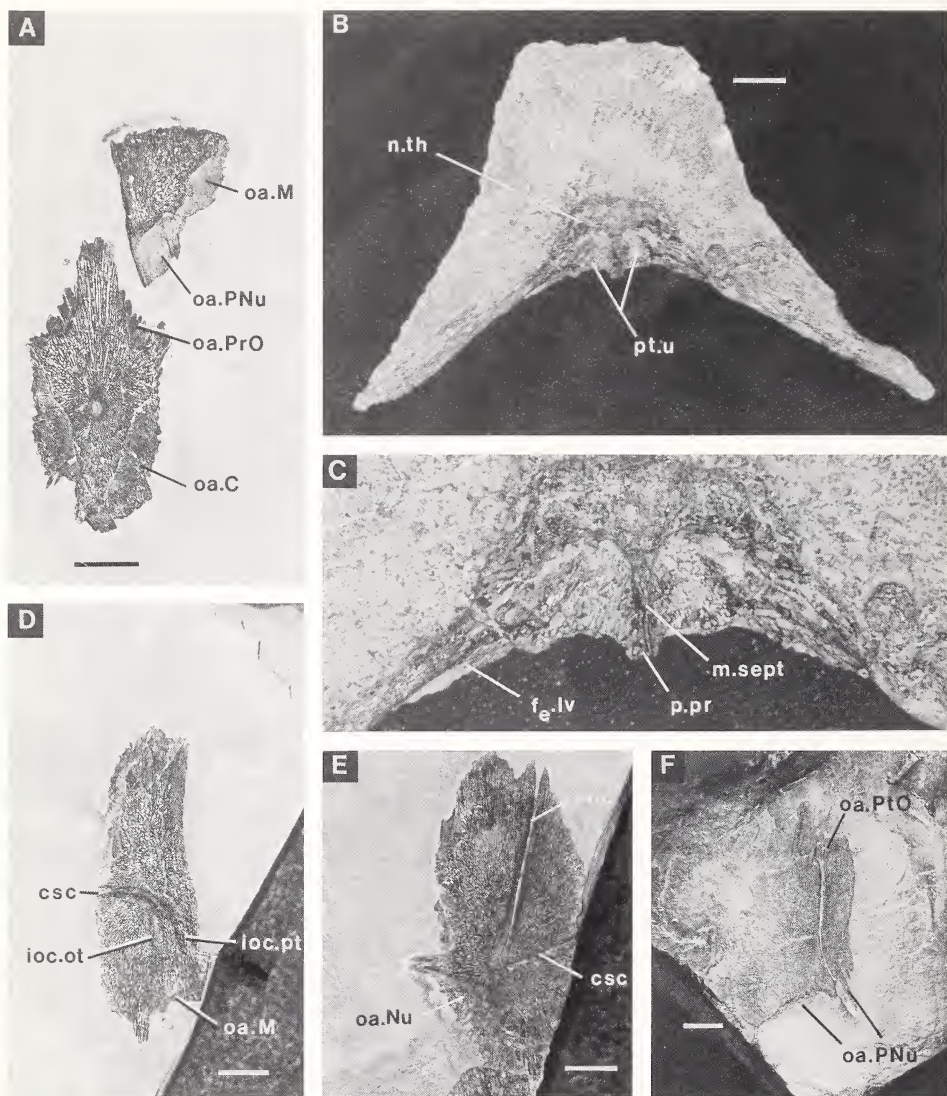


Figure 4. *Gymnotrachelus hydei*. A, pineal (lower left) and left postmarginal plates (CMNH 8052) in external view. B, nuchal plate in internal view and C, close-up of nuchal thickening (CMNH 8051). D, right postorbital plate in external view (CMNH 8052). E, right central plate in external view (CMNH 8052). F, left marginal plate in external view (CMNH 8053). Scale bars equal 1 cm.

sory lines and is directed posteriorly. The angle formed between the otic and postorbital branches is *ca.* 30–40°. Dunkle and Bungart (1939) noted a short postorbital branch of the infraorbital sensory line groove. They suggested that it continued onto the marginal plate based on the presence of a marginal plate overlap area at the termination of the postorbital branch groove (Dunkle and Bungart, 1939, *om.m.*, fig. 2). The interpretation of a marginal plate overlap area and a postorbital process appear to be in error. The putative postorbital process is located well anterior to the supraorbital crista. The overlap area appears to be a depression on the postorbital plate associated with a continuation of the postorbital branch of the infraorbital sensory line. A distinct overlap area for the marginal plate is seen in CMNH 8052 (*oa.M.*, Figure 4D).

The central-postorbital plate length ratio is *ca.* 1.2 (C/PtO). Internally, the supraorbital vault is continued posteriorly. A distinct, low ridge forms the medial boundary of the vault and continues posterolaterally as a supraorbital crista to the lateral margin of the plate. There is no apparent inframarginal crista extending posteriorly from the supraorbital crista on the postorbital plate.

Central (C). The central plates (Figures 2A & B, 3, 4E) are elongate with the posterior margin incompletely preserved in available material. They are separated anteriorly by the pineal plate, are joined along a sinuous suture for *ca.* 33% of their longitudinal length, and are separated posteriorly by the nuchal plate. Two distinct sensory lines are present: a supraorbital sensory line (*soc*, Figure 4E) and a central sensory line (*csc*, Figure 4E). A middle pit-line may be occasionally present and is noted only on CMNH 8054 (seen on the right central plate impression and externally on the left central plate). It is directed posterolaterally from the ossification center forming an angle of *ca.* 35° with the central sensory line. This line appears to be distinct from the “middle head line” of Dunkle and Bungart (1939, *i.ac.sc.*, fig. 1) which, if correctly identified as a sensory line, is more likely a posterior pit-line. A posterior pit-line is not seen on any of the new material and a middle pit-line, as noted above, is found only on CMNH 8054.

A low endolymphatic thickening is present internally at the ossification center and unlike *Dunkleosteus* and *Heintzichthys* is not continuous with the nuchal thickening. The raised ridge indicating the course of the supraorbital sensory line groove on the preorbital plate's internal surface is continued onto the central plate (Figure 3). There is no distinct boundary for the insertion of the cucularis muscle (compare with the depression for the cucularis muscle in *Dunkleosteus*, *dp.m.cu.*, Stensjö, 1963, fig. 112A).

Marginal (M). The marginal plate (Figures 2A & B, 4F) possesses a single sensory groove; a continuation of the postorbital branch of the infraorbital line, which

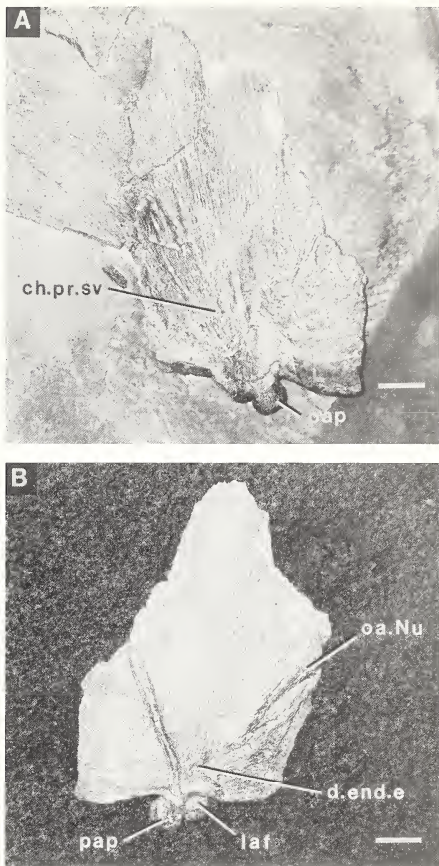


Figure 5. *Gymnotrachelus hydei*. Left paranuchal plate in A, internal and B, external views (CMNH 8051). Scale bars equal 1 cm.

becomes the main lateral line on the paranuchal plate. The boundary between these lines is typically demarcated by the presence of a postmarginal line extending from the ossification center; however, there is no evidence for the presence of a groove for this line in *Gymnotrachelus*. Dunkle and Bungart (1939, p.18, fig. 6A & C) interpreted a single plate fragment with a sensory line as the marginal plate in the holotype (CMNH 5724). This piece is interpreted here as a fragment of the right preorbital

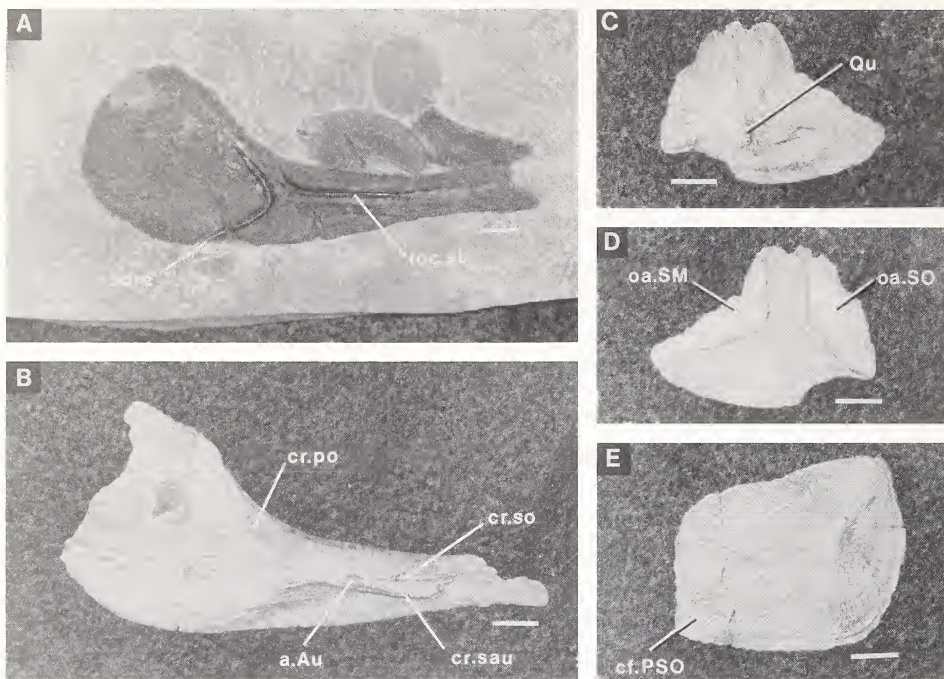


Figure 6. *Gymnotrachelus hydei* (CMNH 8051). Suborbital plate in A, right external and B, left internal views. Right postsuborbital plate in C, internal and D, external views. E, right submarginal plate in internal view. Scale bars equal 1 cm.

plate possessing thickenings associated with the dermal preorbital process. On the marginal plate, the sensory line groove is situated near and parallel to the plate's medial border.

It is difficult to evaluate the presence of a central and marginal plate contact; however, the general spacing of plates suggests a lack of contact. Two overlap areas are present on the marginal plate, an anterior postorbital plate (oa.PtO, Figure 4F) and a posterior paranuchal plate overlap (oa.PNu, Figure 4F). Internally, a low inframarginal crista parallels the external sensory line to the plate's ossification center. At this point, a thickening continues beneath the main lateral line, while the inframarginal crista continues as a low thickening (barely noticeable in CMNH 8051) to the posteroventral corner of the plate and onto the postmarginal plate.

Postmarginal (PM). Two isolated postmarginal plates are preserved, one in CMNH 8052 and the other in CMNH 8799. The postmarginal plate (Figures 2B, 4A) is triangular in shape with anteroventral and posteroventral borders forming a *ca.* 90° angle. A distinctive subobstantic region is absent; however, a thinning of the posteroventral margin is noted in CMNH 8799. The contact margins of neighboring plates are not present in the two specimens with postmarginals preserved, hindering the interpretation of overlap areas. However, the marginal plate shape and orientation of an internal inframarginal crista suggest the presence of overlap areas for the paranuchal (oa.PNu, Figure 4A) and marginal (oa.M, Figure 4A) plates with the latter being larger. Internally, a continuation of the inframarginal crista is present.

Paranuchal (PNu). The paranuchal plate (Figures 2A & B; 5) possesses a postnuchal process that extends onto the descending posterior face of the head shield. An overlap area for the nuchal plate is present (oa.Nu, Figure 5B) which is partially overlain by the postnuchal process forming a recess for the nuchal plate's postero-lateral ala. The main lateral line traverses the plate ending along the posterior margin just above the junction of

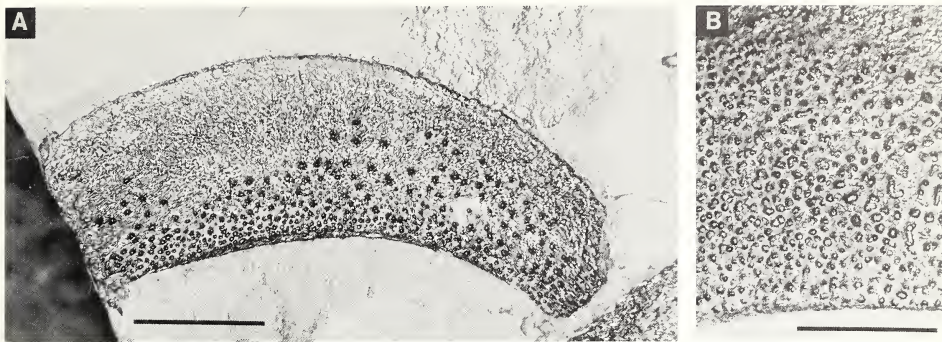


Figure 7. *Gymnotrachelus hydei*. A, sclerotic plate in external view (CMNH 8055). Scale bar equals 1 cm. B, close-up of external ornamentation (CMNH 8051). Scale bar equals 0.5 cm.

the lateral articular fossa (laf, Figure 5B) and occipital para-articular process (pap, Figures 5A & B). An external opening for the endolymphatic duct is present (d.end.e, Figure 5B). The lateral articular fossa is well developed with the occipital para-articular process being short and nearly round.

Internally, there is a distinct channel (ch.pr.sv, Figure 5A) and recess for the dorsal aspect of the supravagial process of the neurocranium. The channel extends posteriorly to the ventral lip of the lateral articular fossa and is directed toward the base of the occipital para-articular process.

Cheek Plates

General features. The three plates (suborbital, postsuborbital, submarginal) of the cheek are not fused to the head shield. As in the head shield, sensory line grooves are bounded by a well-developed lip (ridge). All plates have been flattened secondarily.

Suborbital (SO). The shape of the suborbital plate (Figures 2B, 6A & B) is similar to that of other selenosteids, with the posterior region narrowing gently to form an anterior "handle." The posterior "blade" region is round. The ventral border of the orbit forms a shallow concavity. The groove for the supraoral sensory line (sorc, Figure 6A) forms a closed angle (*ca.* 85°) and does not join with the groove for the suborbital branch of the infraorbital line (ioc.sb, Figure 6A). The suborbital branch groove ends before the anterior extension of the "handle" (a distance of approximately one quarter of the total length of the suborbital plate). The groove parallels the internal suborbital crista (cr.so, Figure 6B) and separates the "handle" into two asymmetrical regions, the ventral region being larger (in *Dunkleosteus* and *Heintzichthys* the position of the groove is closer to the ventral margin).

Internally there is a subocular shelf (cr.so, Figure 6B) and subautopalatine (cr.sau, Figure 6B) and postorbital (cr.po, Figure 6B) cristae. There is no contact face for a

posterior superognathal on the subautopalatine crista. This ventral ridge extends posteroventrally as a low ridge onto the "blade" portion of the suborbital plate (= R3 of Heintz, 1932, fig. 22). The subocular and postorbital cristae are continuous.

Postsuborbital (PSO). The postsuborbital plate (Figures 2B, 6C & D) is triangular with distinct overlap areas for the suborbital (oa.SO, Figure 6D) and submarginal (oa.SM, Figure 6D) plates. The shape of the suborbital overlap reflects the rounded posterior dimensions of the suborbital plate, whereas the submarginal overlap area forms an open angle (*ca.* 100°). These overlaps are separated dorsally resulting in a gap between the suborbital and submarginal plates and the head shield (Figure 2B). An anteroventral notch is present along the postsuborbital plate margin in CMNH 8054 (Figure 6C & D); however, in other specimens, the ventral margin forms a gentle sigmoid curve without a distinctive notch.

On the internal surface, a small thickening denotes the position of the quadrate (Qu, Figure 6C). Above the thickening, two low ridges suggest the trajectory of the palatoquadrate. The quadrate and ridges lie beneath the central region between external overlap areas suggesting that the palatoquadrate traverses beneath the gap between suborbital, postsuborbital, and submarginal plates and head shield.

Submarginal (SM). The submarginal plate (Figures 2B, 6E) is rectangular to subrectangular (in contrast to the elongate submarginal plate of primitive aspinothoracid arthrodires) and loosely abuts an overlap area on the postsuborbital. The ossification center is located postero-dorsally (a posterior location is typical of eubranchyothoracid

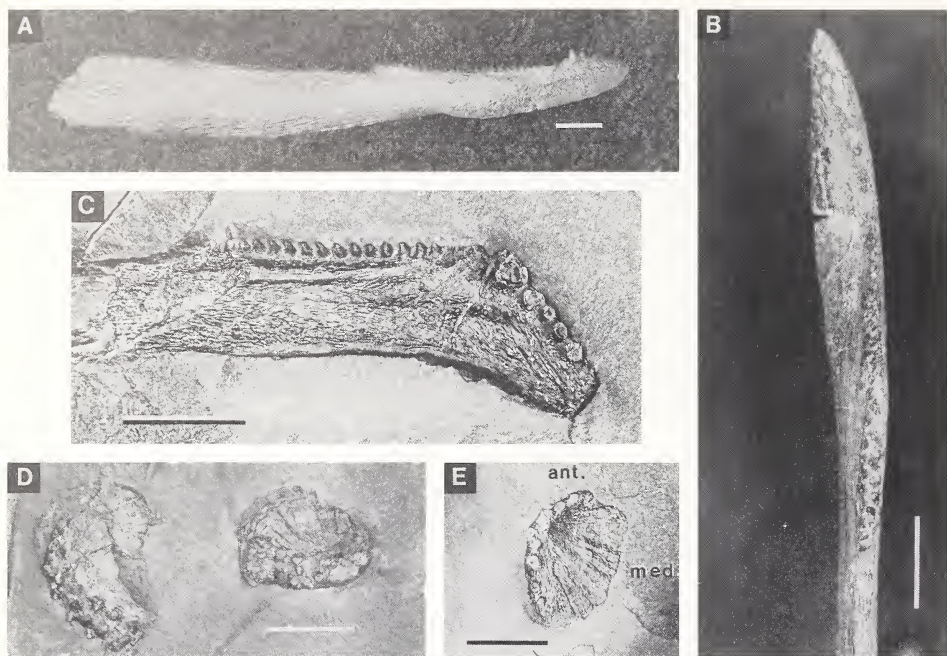


Figure 8. *Gymnotrachelus hydei*. Right inferognathal in A, lateral view and B, close-up of occlusal surface in dorsal view (CMNH 8051). C, close-up of left inferognathal in medial view (CMNH 8776). D, right and left anterior superognathals in ventral view (CMNH 8055). Note paired lateral rows of denticles. E, right anterior superognathal in ventral view (CMNH 8050). Scale bars equal 1 cm.

submarginal plates). Internally, the posterior margin shows growth ridges. A shallow contact face (cf. PSO, Figure 6E) is present at the anteroventral corner. A low ridge is present from the posterodorsal corner through the center of ossification and a short distance beyond. There is no groove for the hyomandibula.

Sclerotic (scler). There are four sclerotic plates (Figures 2B, 7) per eye. Typically, each sclerotic has an external overlap area and an internal contact face at opposite ends for adjacent sclerotic plates, although the nature of contact is variable (e.g., overlap areas at each end or both a contact face and overlap area at one end). Each sclerotic possesses an ornament of punctate denticles (Figure 7). These are densest medially and extend across the surface of the sclerotic. The lateral extent of denticles is variable both within

and between specimens ranging from denticles only on the median edge to complete coverage.

Gnathal Plates and Parasphenoid

General features. Three paired gnathal elements are present (inferognathal, anterior and posterior superognathals). The anterior superognathals do not articulate with the parasphenoid, which is poorly preserved. All plates have been flattened secondarily.

Inferognathal (IG) (Figures 2B, 8A-C). The occlusal and adsymphyseal region occupy ca. 46% of the total inferognathal length (44-48%). Anteriorly, the adsymphyseal region possesses 5-6 large denticles in a single row. Typically the largest denticle is found at the posterior apex of the adsymphysis. Posterior to this cusp, the occlusal surface possesses a single row of evenly spaced denticles extending to the posterior margin of the occlusal region. The anterior denticles are recurved where not worn. In the posterior 40% of the occlusal region, one or two additional lateral rows of denticles are present (Figure 8B & C). The denticles within an individual inferognathal are spaced equally along the occlusal surface (5-10 denticles per centimeter). The number of denticles per centimeter varies inversely with overall size, and therefore

varies with age of the individual.

Anterior superognathal (ASG). The anterior superognathal (Figures 8D & E, 9A) is oval with 7-9 denticles arranged along the anterior and lateral margins. The anterior 3-4 denticles form an angle with the posterolateral denticles of *ca.* 120-130°. Anterior denticles typically form a single row with occasional accessory denticles. The lateral row is often bifid with denticles in each fork occasionally possessing up to two accessory denticles (Figure 8D; CMNH 8050 has only a single lateral row, Figure 8E). The bulk of the plate is represented by a medial lamina. A posterior process is absent.

Posterior superognathal (PSG). The posterior superognathals (Figure 9A) are elongate and crescent shaped. They are triangular in cross-section with the apex located dorsolaterally. A single row of denticles is located on the lateral convex margin of the flattened ventral surface (Figure 9A). Denticle number is variable and often difficult to discern due to worn or missing denticles (19-29 denticles; 3-5 denticles per centimeter anteriorly and 5-8 posteriorly; the 18 denticles reported by Dunkle and Bungart, 1939, represent an incomplete plate). At *ca.* 40% of the total length from the anterior margin, there is a shallow "step" extending from the ossification center anteromedially (Figure 9A). This "step" separates the lower and wider anterior region from the posterior region (the "step" may be homologous to the posterior process of the posterior superognathal plate in other arthrodires).

No single specimen possesses a complete inferognathal and set of superognathals. Anterior and posterior superognathals from CMNH 8055 and 8053 equal or exceed combined dimensions for adsymphyseal and occlusal regions in any single inferognathal. This suggests that the anterior and lateral denticles of the anterior superognathal occlude with the adsymphyseal region of the inferognathal. The most posterior denticles probably extend just beyond the apical denticle of the inferognathal (this is comparable to the condition in *Dunkleosteus* where the anterior superognathal occludes anteromedially and posterior to the anterior cusp of the inferognathal). The inferognathal adsymphyseal denticles probably fit between the two posterior rows of denticles on the anterior superognathal. Denticles of the posterior superognathal occlude with the main inferognathal occlusal surface.

Parasphenoid. An incomplete and poorly preserved plate is interpreted as a parasphenoid in CMNH 8052 (Figure 9B). The parasphenoid is ovate leaf-like in shape with a short "stem" and a long narrow "leaf" (overall length/width = *ca.* 2.6). On the basis of comparisons with *Melanosteus* (Lelièvre et al., 1987), the "stem" is interpreted as the prehypophyseal region (pre.reg, Figure 9B). The specimen is preserved in dorsal view with most of the plate missing revealing an impression of the ventral surface. Several punctate depressions suggest the presence of denticles.

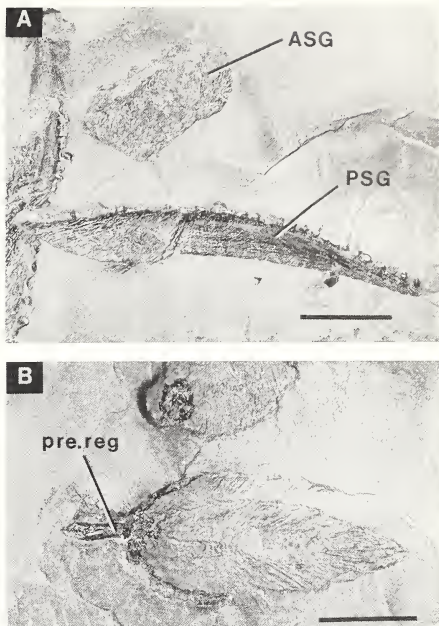


Figure 9. *Gymnotrachelus hydei*. A, left posterior superognathal in ventral view and an anterior superognathal in dorsal view (CMNH 8053). B, incomplete parasphenoid in dorsal view showing an impression of the ventral surface (CMNH 8052). Scale bars equal 1 cm.

Dermal Shoulder Girdle

General features. The dermal shoulder girdle is composed of 17 individual plates: three unpaired median plates (median dorsal, anterior and posterior median ventrals) and seven paired plates (anterior dorsolateral, posterior dorsolateral, anterior lateral, posterior lateral, anterolateral, anterior and posterior ventrolaterals). The spinal plate is assumed to have been lost phylogenetically. A poorly preserved anterolateral is recognized in a single specimen. Lateral line grooves possess a well-developed lip. All plates have been flattened secondarily.

Median dorsal (MD). The median dorsal plate (Figures 2A & B, 10) is rounded posteriorly with a small median process. The anterior margin forms a rounded W-shape with a central process ranging from *ca.* 16.7% (CMNH 8049) to *ca.* 60% (CMNH 8051) the length of the lateral alae. A lateral embayment is formed at the junction of the anterior ala and posterior rounded region. These embay-

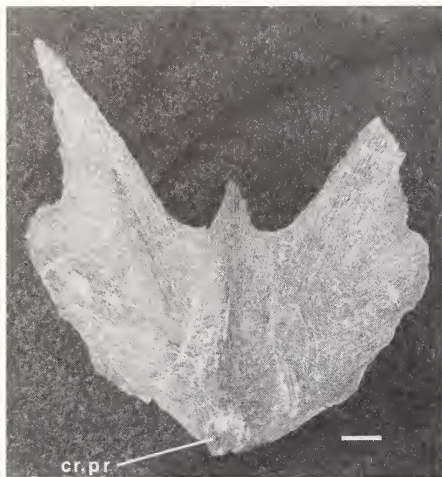


Figure 10. *Gymnotrachelus hydei* (CMNH 8052). Median dorsal plate in ventral view. Scale bar equals 1 cm.

ments are reminiscent of the condition seen in *Titanichthys* and *Bungartius* (Denison, 1978, fig. 80 and fig. 81 respectively). The projecting anterolateral corners of the posterior region overlap the posterior dorsolateral plates.

A carinal process (cr.pr, Figure 10) projects beyond the posterior border of the median dorsal plate. Internally, the carinal process begins as a low thickening on the central anterior process. The carinal process lacks a posterior concavity (spatulate forms include, e.g., *Dunkleosteus* and *Heintzichthys*). Beginning at the posterior third, the keel possesses a ventral groove that extends onto the posterior process. The median dorsal plate is further strengthened internally by paired thickenings radiating from the posterior base of the carinal process to the paired alae and along the posterolateral margins to the anterior areas of overlap for the posterior dorsolateral plates (to the rounded processes just posterior to the lateral notches). Contact faces are not discernible.

Anterior dorsolateral (ADL). The anterior dorsolateral plate (Figures 2A & B; 11D) carries the continuation of the main lateral line groove. Two overlap areas are present: a narrow anterodorsal area for the ala of the median dorsal plate (oa.MD, Figure 11D) and an anteroventral area for the anterior lateral plate (oa.AL, Figure 11D). The overall shape is difficult to infer since the thin posterior margin is incomplete. Piecing together a shape based on overlap areas on adjacent plates (CMNH 8051) suggests that the posterior margin is three-pronged (dorsal,

middle, and ventral extensions). First, there is a dorsal extension possessing the median dorsal overlap and contacting the posterior dorsolateral plate. Second, a middle extension lies within the anterior dorsolateral overlap area on the posterior lateral plate (this overlap is variable in some specimens suggesting less of a distinction between the dorsal and middle extensions on the posterior margin of the anterior dorsolateral plate). Finally, there is a ventral extension possessing an overlap area for the anterior lateral plate. On the anterior margin, there is a well-developed condyle (kd, Figure 11D). Internally, a subglenoid process is present.

Posterior dorsolateral (PDL). The posterior dorsolateral plate (Figures 2A & B, 11C) is triangular (height/base = ca. 2.4 measured along the greatest dimension and its perpendicular dimension at the base). The posterior margin possesses a shallow process. Two distinct overlap areas are present on the external surface, an anterodorsal area for the median dorsal plate (oa.MD, Figure 11C) and an anteroventral one for the anterior dorsolateral plate (oa.ADL, Figure 11C). Both the posterior dorsolateral and posterior lateral plates in CMNH 8051 (Figure 11C & E) possess depressed regions on their external surfaces associated with their junction. Although there appears to be an overlap area on the posterior dorsolateral plate for the posterior lateral plate, this depression most likely represents a secondarily collapsed recess for the insertion of the posterior lateral plate (rec.PL, Figure 11C).

Anterior lateral (AL). The anterior lateral plate (Figures 2B, 11A & B) is widest dorsally and tapers to the anteroventral angle (av.v, Figure 11A). There is no evidence for the presence of a spinal plate. A medial lamina is present below a variably thickened postbranchial embayment (th.pbe, Figure 11A; erroneously labeled "prebranchial thickening" in Carr, 1991). A small pointed process extends anteriorly from the postbranchial thickening (Figure 11B, broken off, but reconstructed based on other specimens). Internally, the anterodorsal margin is thickened where the plate contacts the overlap area on the anterior dorsolateral plate. A small recess (rec, Figure 11B, partially obscured by a pyrite nodule, pyr., Figure 11B) is formed between the anterodorsally thickened margin and the pointed process on the postbranchial thickening. This recess probably housed the posteroventral corner of the head shield.

Posterior lateral (PL). The posterior lateral plate (Figures 2B, 11E) is taller than wide (height/width = ca. 1.7 along greatest dimension). The posterior margin possesses a rounded process. Anteroventrally, there are overlap areas for the anterolateral (oa.AL, Figure 11E) and anterior dorsolateral (oa.ADL, Figure 11E) plates (on the type specimen the anterolateral overlap is expanded dorsally and may be continuous with an overlap for the posterior dorsolateral plate). The dorsal apex is involved in a

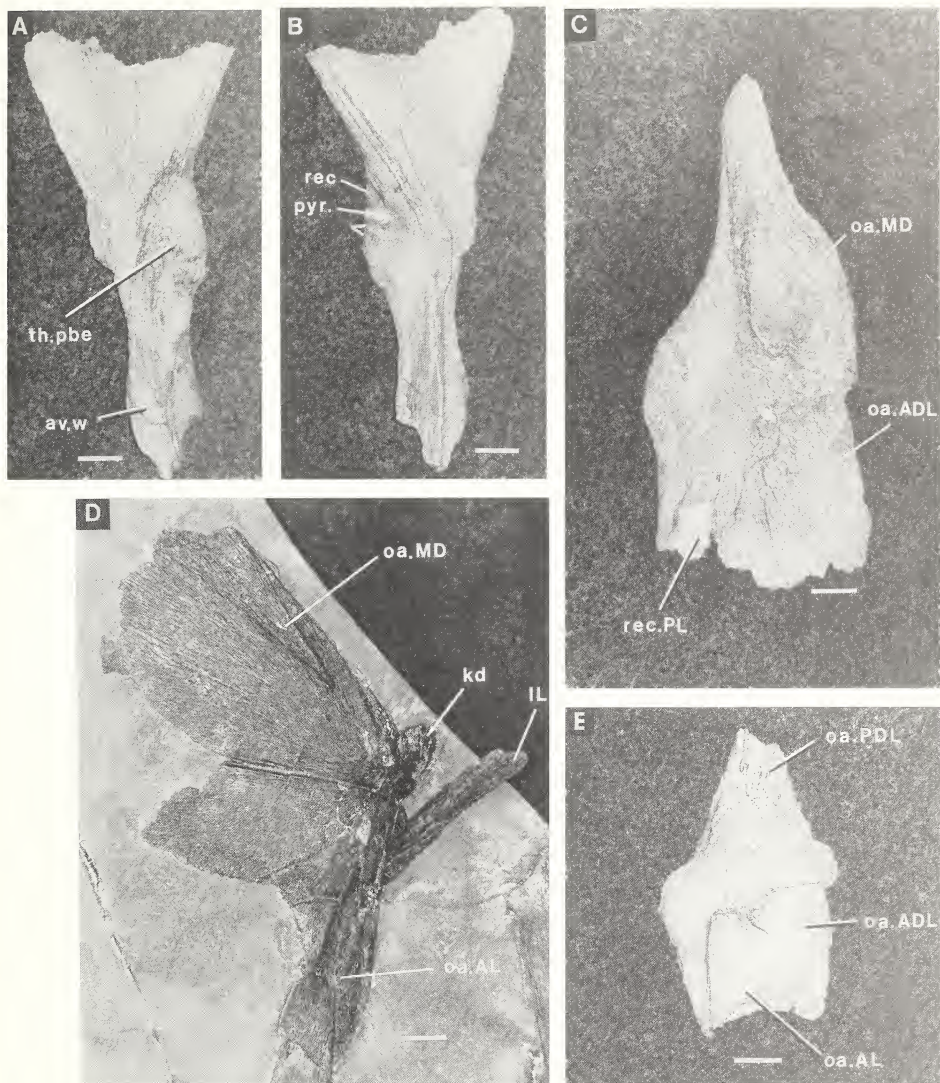


Figure 11. *Gymnotracheus hydei* (CMNH 8051). Right anterior lateral plate in A, external and B, internal views. Note that the short process forming the anteroventral border of the recess is reconstructed in white. C, right posterior dorsolateral plate in external view. D, right anterior dorsolateral plate in external view and interolateral plate. E, right posterior lateral plate in external view. Scale bars equal 1 cm.

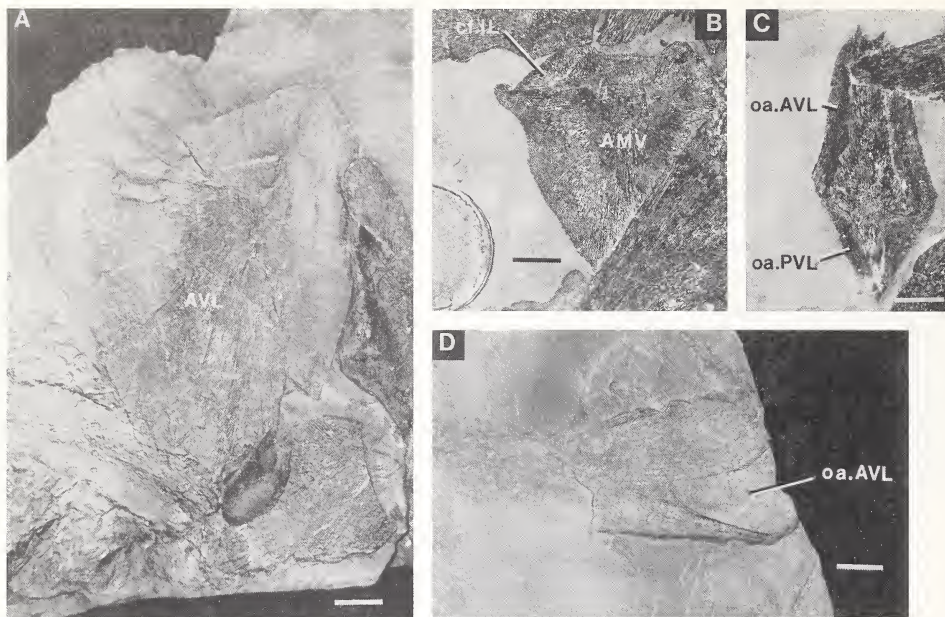


Figure 12. *Gymnotrachelus hydei*. A, right anterior ventrolateral plate in internal view (CMNH 8054). B, anterior median ventral plate in internal view (CMNH 8050). C, posterior median ventral plate in external view (CMNH 8050). D, anterior fragment of left posterior ventrolateral plate in external view (CMNH 8054). Scale bars equal 1 cm.

junction with the posterior dorsolateral plate (oa.PDL, Figure 11E). The exact nature of this junction is unclear, but as noted above may have involved an insertion of the posterolateral plate into the posterior dorsolateral plate (a similar style of junction is seen in *Dmkleostens*).

Interolateral (IL). A single example of an interolateral plate is seen in CMNH 8051 (Figure 11D). Little can be discerned other than the presence of an elongate plate.

Anterior median ventral (AMV). An anterior median ventral plate (Figures 2C, 12B) is present in CMNH 8050 only and is partially covered and exposed in internal view. The plate is triangular in shape with the base of the triangle anterior (width/length = *ca.* 1.0). The anterior margin possesses two anteriorly directed and rounded projections separated medially by a shallow trough. A contact face for the interolateral plate (cf. IL, Figure 12B) is present laterally on the anterior margin. The anterolateral corners of the plate form short processes. From these processes, the

plate narrows to its posterior midpoint with gently convex lateral margins. Compression during preservation of the anterior median ventral plate reveals the presence of large overlap areas for the anterior ventrolateral plates on the external surface.

Posterior median ventral (PMV). The posterior median ventral plate (Figures 2C, 12C) is diamond shaped (length/width = *ca.* 2.2). Anterior ventrolateral plate overlap areas (oa.AVL, Figure 12C) extend *ca.* 66% the length of the posterior median ventral plate with overlap areas for the posterior ventrolateral plates (oa.PVL, Figure 12C) extending the remaining portion of the plate. The posterior overlap area is deeper than the anterior one reflecting the overlap pattern of the anterior and posterior ventrolateral plates (the posterior ventrolateral plate overlies the anterior ventrolateral plate).

Anterior ventrolateral (AVL). The anterior ventrolateral plate (Figures 2C, 12A) is longer than wide (length/width = *ca.* 1.3) with the greatest width opposite the ossification center (it is noteworthy that the plate shape and presence of growth ridges strongly resemble the posterior ventrolateral plate in *Heintzichthys gouldii*, Carr, 1991, fig. 14B. There is no question as to the correct interpretation of plates in both forms based on overlap patterns). A thickening is present at the ossification center; however, the Y-shaped thickenings seen in other forms are not discernible (e.g.,

seen in *Eastmanosteus calliaspis*, Dennis-Bryan, 1987, and *Heintzichthys gouldii*, Carr, 1991). Concentric growth ridges are present on the internal surface.

Posterior ventrolateral (PVL). There are no complete posterior ventrolateral plates (Figures 2C, 12D) that clearly show both an anterior and posterior margin (with the possible exception of a right plate with a dislocated posterior fragment on CMNH 8049). CMNH 8799 possesses nearly complete plates with the posterior portion missing. This specimen shows the posterior ventrolateral plates to be greater than three times longer than wide (length/width = ca. 3.3). CMNH 8049 is nearly five times longer than wide (length/width = ca. 4.9) and appears to represent a younger specimen with fewer growth ridges on the posterior ventrolateral plate. On the basis of CMNH 8049, the posterior ventrolateral plate tapers to a fine posterior point. Ossification centers are located at midplate close to the medial margin.

Internally, growth ridges are present and on CMNH 8049 a contact face for the left posterior ventrolateral plate is present on the medial margin of the right plate (this overlap pattern is opposite to that seen in *Dunkleosteus* and *Heintzichthys*, Carr, 1991, fig. 12B). Externally there is an anterior ventrolateral plate overlap area which is exposed in CMNH 8054 only (oa.AVL, Figure 12D). Similar elongate posterior ventrolateral plates are seen in an undescribed selenosteoid from the Cleveland Shale.

Pectoral and Pelvic Fins, Axial Skeleton, and Neurocranium

General features. The pelvic fins, axial skeleton, and neurocranium are not preserved. A perichondrally ossified scapulocoracoid is present. Additional unidentifiable perichondral fragments are present.

Scapulocoracoid. Recognizable scapulocoracoids are present in CMNH 8047 and CMNH 8799. Although incomplete and highly fragmented, the scapulocoracoid appears to be relatively large and nearly equidimensional (length/height = ca. 1.1). Numerous neurovascular foramina are present on both the internal and external surfaces. An articular ridge and basals are not discernible on the available material.

Phylogenetic Discussion

The relationships of the North American genera of selenosteoid arthrodires remain unresolved. Dunkle and Bungart (1939) noted affinities between *Gymnotrachelus* and *Stenosteus*, *Selenosteus*, *Trachosteus*, and *Mylostoma*, although they deferred any definitive assignment. Lelièvre et al. (1987) suggested a sister group relationship between *Gymnotrachelus* and European selenosteids, in part, but did not consider the remaining North American selenosteids. Carr (1991) suggested that *Gymnotrachelus* is a member of an unresolved multi-

chotomy with other aspinothoracid arthrodires and proposed that *Selenosteus* is related more closely to European forms (*Gorgonichthys*, *Heintzichthys*, *Gymnotrachelus* (*Selenosteus* (*Pachyosteus*, *Rhinosteus*))). Denison (1978) noted the uniqueness of European and North American forms, but it is not clear whether he is suggesting that North American forms are monophyletic or is suggesting a relationship equivalent to those proposed by Lelièvre et al. (1987) or Carr (1991). Each of the above hypotheses is consistent with the hypothesis that North American and European selenosteids represent distinct monophyletic groups, but none provide conclusive evidence. Lelièvre et al. (1987) failed to analyze additional North American taxa. Carr (1991), while adding an additional North American taxon, failed to include most of the European forms. Denison (1978), in suggesting the monophyly of these two groups, failed to provide any diagnosis or phylogenetic analysis. While a final revision of selenosteoid arthrodires must await the additional description of unpublished North American materials and a review of European selenosteids, new material for *Gymnotrachelus* allows a more definitive analysis of its position within the clade.

An analysis of nine aspinothoracid arthrodiran taxa (after Lelièvre et al., 1987: *Gymnotrachelus*, *Melanosteus*, *Rhinosteus*, *Pachyosteus*, *Enseosteus*, *Microsteus*, *Braunosteus*, Brachydeiridae, and Trematosteidae) using 15 characters gives two equally parsimonious trees (exhaustive search option, treelength = 19, consistency index = 0.737). Trematosteidae and Brachydeiridae are designated as outgroup members.

Characters 1-14 are taken from Lelièvre et al. (1987) with one additional character added to the analysis and are as follows:

1. Submarginal plate shape and orientation (Lelièvre et al., 1987): elongate (0); raised and reduced (1).
2. Postnasal plate fused to preorbital plate (Lelièvre et al., 1987): absent (0); present (1).
3. Marginal plate forms part of orbit margin (Lelièvre et al., 1987): absent (0); present (1).
4. Position of the preorbital-postorbital-central plate junction (Lelièvre et al., 1987): at a level over the anterior half of the orbit (0); posterior half of orbit (1).
5. Angle formed by the postorbital and otic branches of the infraorbital sensory line grooves (Lelièvre et al., 1987): open (0); closed (1).
6. Length of cheek and head shield contact, independent of overlapping or fusion of these two dermal units (Lelièvre et al., 1987): long (0); short (1).
7. Nature of inferognathal and posterior superognathal occlusal surfaces (Lelièvre et al., 1987): trencant or rounded (0); denticulate (1).
8. Posterior ventrolateral and posterior median plates (Lelièvre et al., 1987): present (0); absent (1).

9. Position of the dermal articulation between the head and thoracic shields (modified from Lelièvre et al., 1987): dorsolateral (0); displaced ventrally (1).
10. Dorsal process on the posterior superognathal plate (Lelièvre et al., 1987): present (0); absent (1).
11. Form of the anterior lateral plate (Lelièvre et al., 1987): infraobstantic region of plate short (0); infraobstantic and postbranchial region elongate with the dorsal region narrow (1).
12. Lingiform process on the suborbital plate (modified from Lelièvre et al., 1987): present (0); reduced (1). This character has been scored as in Lelièvre et al. (1987), although absence of a lingiform process is reinterpreted here as a reduction. The presence of a lingiform process may represent a plesiomorphic feature for the aspinothoracid arthrodires. Recognition of this process in lateral view may reflect the size of the subautopalatine crista (cr.sau, Figure 6B; Carr, 1991) and whether, when secondarily flattened during preservation, the process extends below the ventral external border of the suborbital plate. This crista is often thin and easily lost unless reinforced to form a contact face with the posterior superognathal as seen in *Dunkleosteus* and *Eastmanosteus calliaspis* (cf. PSG, Carr, 1991, fig. 7B).
13. Overlap between the head and cheek dermal plates (Lelièvre et al., 1987): absent (0); present (1).
14. Prehypophyseal region of parasphenoid plate elongate and stem-like (modified from Lelièvre et al., 1987): absent (0); present (1).
15. Supraethmoid thickening (th.seth, Stensiö, 1963, figs. 113A, B): absent (0); present (1).

A data matrix for the nine taxa and 15 characters used in the current analysis is provided below. ? = missing data; - = case where the character is not applicable.

Trematosteidae	1 1 0 1 0	0 0 0 0 0	0 0 0 0 0
Brachydeiridae	1 0 1 1 0	0 0 1 0 0	0 0 1 0 ?
<i>Gymnotrachelus</i>	1 - 0 0 1	1 1 0 0 1	1 1 0 1 0
<i>Enseosteus</i>	1 0 1 0 1	1 1 0 1 0	0 0 ? 0 1
<i>Microsteus</i>	1 0 1 0 1	1 1 0 1 0	0 1 1 0 1
<i>Pachyosteus</i>	1 0 1 0 1	1 1 0 0 1	0 0 1 0 ?
<i>Rhinosteus</i>	1 0 1 0 1	1 1 0 0 1	1 1 1 0 ?
<i>Melanosteus</i>	? 0 ? 0 1	1 1 0 0 1	1 1 ? 1 1
<i>Braunosteus</i>	? 1 1 0 0	0 0 0 0 0	0 0 1 0 ?

Family Selenosteidae

(Selenosteidae Dean, 1901; Pachyosteidae Gross, 1932; Selenosteidae Stensiö, 1959, and Rhinosteidae Stensiö, 1963; Selenosteidae Denison 1978; Selenosteidae Lelièvre et al., 1987)

Selenosteidae is a subgroup of the monophyletic aspinothoracid arthrodires (Miles and Dennis, 1979; Gardiner and Miles, 1990; Carr, 1991; but contrast Denison, 1984) that shares with other members of this larger clade a reduction of the lateral and occipital thickenings of the head shield and loss of the spinal plate (Carr, 1991). Denison (1978) united *Braunosteus*, *Enseosteus*, *Microsteus*, *Pachyosteus*, *Rhinosteus*, *Gymnotrachelus*, *Paramylostoma*, *Selenosteus*, and *Stenosteus* in the family Selenosteidae based on the presence of large orbits, long central plates (relative to preorbitals), short submarginal plates, and a large nuchal gap between the head and thoracic shields. Lelièvre et al. (1987) analyzed better known members of this clade (*Gymnotrachelus*, *Melanosteus*, *Rhinosteus*, *Pachyosteus*, *Enseosteus*, *Microsteus*, and *Braunosteus*) along with the outgroups Trematosteidae and Brachydeiridae and excluded *Braunosteus* from the Selenosteidae.

Although a full comparison of analyses by Lelièvre et al. (1987) and Carr (1991) is not practical at present since many of the additional characters used by Carr cannot be evaluated readily using published accounts, some patterns do emerge. The character analyses for *Gymnotrachelus* by Lelièvre et al. (1987) were limited by the material available at the time (the holotype described by Dunkle and Bungart, 1939). Dunkle and Bungart's (1939) reconstruction and plate identifications were flawed, in part, due to poor preservation. Seven of 14 characters interpreted by Lelièvre et al. (1987, characters 1, 6, 7, 10-12, 14) as being primitive are seen to be derived, on the basis of more complete material. Consequently, the analysis of phylogenetic relationships is altered. *Gymnotrachelus* is now recognized as a derived member of the selenosteid clade. A phylogenetic analysis of the taxa reviewed by Lelièvre et al. (1987; Trematosteidae and Brachydeiridae here set as outgroups) suggests the following relationships: (Trematosteidae, Brachydeiridae, *Braunosteus*) ((*Microsteus*, *Enseosteus*) (*Pachyosteus*, (*Rhinosteus* (*Melanosteus*, *Gymnotrachelus*))).

Lelièvre et al. (1987) and the current study concur that the group Selenosteidae *sensu* Lelièvre et al. (1987; Figure 13) is characterized by the presence of: (1) enlarged orbits associated with a closed angle between the postorbital and otic branches of the infraorbital sensory line and a reduction of the contact between the cheek and head shield (characters 5 and 6, Lelièvre et al., 1987) and (2) inferognathals and posterior superognathals possessing denticles along their occlusal surfaces in adults (character 7, Lelièvre et al., 1987).

Within the family, *Melanosteus* and *Gymnotrachelus* are united by the presence of a parasphenoid with a narrow stem-like prehypophyseal region (Figure 13; character 14, modified from Lelièvre et al., 1987).

Synapomorphies uniting *Rhinosteus* with the previous clade (*Melanosteus* and *Gymnotracheilus*) are the form of the anterior lateral plate (elongate and dorsally narrow; Figure 13; character 11, Lelièvre et al., 1987) and reduction of the linguiform process on the suborbital plate (Figure 13; character 12, modified from Lelièvre et al., 1987, who in contrast consider the loss of a linguiform process). The definition for a linguiform process needs refinement to distinguish between a subautopalatine crista (cf. sau, Figure 6B; see also Carr, 1991) and a linguiform process that appears to include a ventrally visible subautopalatine crista, which may or may not possess reinforcement for a posterior superognathal contact face (cf. PSG, Carr, 1991, fig. 7B).

Uniting *Pachyosteus* with the above clade is the loss of a dorsal process on the posterior superognathal (Figure 13; character 10, Lelièvre et al., 1987).

Microsteus and *Enseosteus* share a ventral position for the dermal articulation between the head and thoracic shields (Figure 13; character 9, Lelièvre et al., 1987; see also Miles, 1969). Additionally, they possess a supraethmoid thickening (character 15; th.seth, Stensiö, 1963, fig. 113A & B; independently derived in *Melanosteus*, Lelièvre et al., 1987, fig. 3). The presence of this feature is primitive, with Trematosteidae and *Gymnotrachelus* independently losing the supraethmoid thickening. However, members of immediate outgroups (e.g., *Dunkleosteus* and *Heintzichthys*) lack a supraethmoid thickening. Based on a parsimony argument, the presence of a supraethmoid thickening is a derived feature known only in *Enseosteus*, *Microsteus*, and *Melanosteus*. This region of the head shield is not known in Brachydeiridae, *Rhinosteus*, *Pachyosteus*, and *Braunosteus*.

One of the two equally parsimonious trees derived from the current study contains a monophyletic Selenosteidae *sensu* Denison (1978), which includes *Braunosteus*. The alternative hypothesis agrees with Lelièvre et al. (1987) placing Brachydeiridae as the sister group to selenosteids, but leaves unresolved the relationship of *Braunosteus*. Selenosteidae *sensu* Denison (1978) is characterized by an anterior shift of the triple point formed by the junction of central, preorbital, and postorbital plates (character 4, Lelièvre et al., 1987). In the alternative tree, a Brachydeiridae-Selenosteidae clade is characterized by the loss of fusion between the postnasal plate and head shield. The latter hypothesis suggests that fusion of the postnasal is a primitive feature. As noted above for the supraethmoid thickening, a consideration of additional outgroups suggests that the fusion of the postnasal plate represents a derived feature which is either independently evolved in Trematosteidae and *Braunosteus* or represents a synapomorphy for the two taxa. The absence of fusion in basal eubrachyothoracic arthrodires gives a weak criterion for choosing between

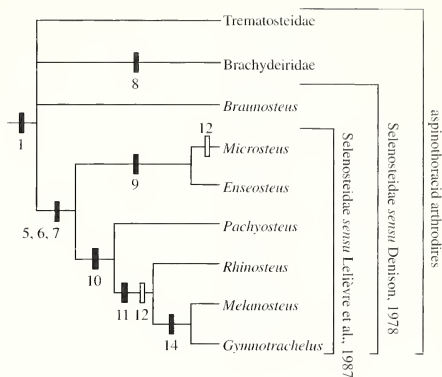


Figure 13. A strict consensus tree based on two trees derived from PAUP (two trees found with exhaustive search, treelength = 19, consistency index = 0.737). Trematosteiidae and Brachydeiridae are designated as out-group members. Unambiguous character transformations are indicated as follows: unique, black filled rectangles and homoplasious, open rectangles. Characters 1 and 8 are uninformative.

these two equally parsimonious trees. Selenosteidae *sensu* Denison may represent a more appropriate depiction of the relationship of *Braunosteus* (i.e., a basal selenosteid arthrodire). The phylogenetic position of *Braunosteus* is sensitive to the choice of additional outgroups. A final resolution of the relationship of *Braunosteus* is beyond the scope of this paper.

Denison (1978) considered three additional North American taxa as members of the Selenosteidae that are not considered in the current study (*Selenosteus*, *Stenosteus*, and *Paramylostoma*). *Selenosteus* and *Stenosteus* share with *Gymnotrachelus* a uniquely shaped median dorsal plate with pronounced anterolateral alae. This feature might suggest a close relationship among these taxa. *Paramylostoma*, the remaining selenosteid which is represented by only a few specimens, is too poorly known to analyze adequately. The loss of a posterior process on the posterior superognathal suggests that *Paramylostoma* may be a member of the *Pachyosteus-Rhinosteus-Melanosteus-Gymnotrachelus* group (Figure 13), although this assignment is tenuous at best.

Conclusion

New material for *Gymnotrachelus* affords better resolution of its phylogenetic position within Selenosteidae.

Gymnotrachelus is a derived member of Selenosteidae and is the sister group to *Melanosteus*. The present study has not resolved adequately the relationships of *Braunosteus*, although among alternative hypotheses a parsimony argument suggests that *Braunosteus* is a basal member of Selenosteidae. Analysis of other putative members of Selenosteidae (*Selenosteus*, *Stenosteus*, *Paramylostoma*) is only tentative and further analysis must await a review of poorly known taxa and description of new materials. *Selenosteus* and *Stenosteus* are speculatively related to *Gymnotrachelus* while *Paramylostoma* appears to be a member of the *Pachyosteus-Rhinosteus-Melanosteus-Gymnotrachelus* clade.

Acknowledgments

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Abbreviations Used in Text and Figures

a.Au	depression for autopalatine
ADL	anterior dorsolateral plate
AL	anterior lateral plate
AMV	anterior median ventral plate
ant.	anterior
ASG	anterior superognathal
AVL	anterior ventrolateral plate
av.w	anteroventral wing
C	central plate
cf.IL	contact face for interolateral plate
cf.PSO	contact face for postsuborbital plate
ch.pro.pr	channel for dorsal aspect of preorbital process of neurocranium
ch.pr.sv	channel for dorsal aspect of supravagal process of neurocranium
cr.po	postocular crista

cr.pr	carinal process	oa.SO	overlap area for suborbital plate
cr.sau	subautopalatine crista	P	pineal plate
cr.so	subocular crista	pap	occipital para-articular process
csc	central sensory line groove	PDL	posterior dorsolateral plate
d.end.e	external opening for the endolymphatic duct	PL	posterior lateral plate
f _e .lv	elongate fossa for levator muscle of head	PM	postmarginal plate
IG	inferognathal	PMV	posterior median ventral plate
IL	interolateral plate	PNu	paranuchal plate
ioc.ot	otic branch of infraorbital line groove	pp	posterior pit-line groove
ioc.pt	postorbital branch of infraorbital line groove	p.pr	median posterior process
ioc.sb	suborbital branch of infraorbital line groove	pre.reg	prehypophysial region
kd	glenoid condyle	PrO	preorbital plate
laf	lateral articular fossa	PSG	posterior superognathal
lc	main lateral line	PSO	postsuborbital plate
M	marginal plate	PtO	postorbital plate
MD	median dorsal plate	pt.u	paired pits on visceral surface of nuchal plate
med.	medial	PVL	posterior ventrolateral plate
m.sept	median septum	pyr.	pyrite nodule
n.th	nuchal thickening	Qu	position of quadrate
Nu	nuchal plate	R	rostral plate
oa.ADL	overlap area for anterior dorsolateral plate	rec	recess
oa.AL	overlap area for anterior lateral plate	rec.PL	collapsed recess for the posterior lateral plate
oa.AVL	overlap area for anterior ventrolateral plate	scler	sclerotic plate
oa.C	overlap area for central plate	SM	submarginal plate
oa.M	overlap area for marginal plate	SO	suborbital plate
oa.MD	overlap area for median dorsal plate	soc	supraorbital sensory line groove
oa.Nu	overlap area for nuchal plate	sorc	supraoral sensory line groove
oa.PL	overlap area for posterior lateral plate	suov	supraorbital vault
oa.PNu	overlap area for paranuchal plate	th.pbe	thickening within the postbranchial embayment
oa.PrO	overlap area for preorbital plate	?	unknown plate fragment
oa.PtO	overlap area for postorbital plate	1	postscript denoting a left element
oa.PVL	overlap area for posterior ventrolateral plate	2	postscript denoting a right element
oa.SM	overlap area for submarginal plate		

KIRTLANDIA[®]

The Cleveland Museum of Natural History

February 1994

Number 48:23-30

PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

OPENING REMARKS

MARY LOU FERBERT

*Trustee, The Cleveland Museum of Natural History
1 Wade Oval Drive, University Circle
Cleveland, OH 44106-1767*

Tonight we are assembled to honor Dr. Stephen Jay Gould, who is the recipient of The Cleveland Museum of Natural History's first David S. Ingalls, Jr. Award for Excellence—named for our esteemed past president. The range of Dr. Gould's honorary degrees, fellowships, literary awards, and academic medals is overwhelming. Perhaps it is The Cleveland Museum of Natural History that is being honored tonight by this man's presence. Dr. Gould, it is indeed a privilege and a pleasure to have you here.

I would like to touch briefly on some of the reasons Stephen Jay Gould surfaced so quickly in our survey of candidates for this new award.

Scientific inquiry is a dynamic process that involves questioning, hypothesizing, and re-examining accepted principles — again and again — probing for the truth in the murky haze of evidence we gather in our effort to understand the natural systems of our planet. This is the approach to research of a great scientist. And Dr. Stephen Jay Gould is a great scientist. When he was 31, Dr. Gould, in collaboration with Dr. Niles Eldredge, published "Punctuated Equilibria: An Alternative to Phyletic Gradualism." Their new theory of punctuated equilibrium, proposing that evolution proceeds by a series of fits and starts, was extremely controversial for it challenged the scientific orthodoxy of phyletic gradualism. Eldredge and Gould's theory soon, however, gained prominence.

Questioning is a quality that we wish for in our young

students, for it is controversy that drives the scientific community — both believers and challengers — to dig deeper, to re-evaluate.

Dr. Gould is not just a respected scholar, he is a prolific writer of great wit. I'm sure many in the audience tonight had their curiosity whetted and their minds stimulated by one or more of Dr. Gould's books, essays, or his monthly columns in *Natural History* magazine. At a dinner party within the past month I was delighted to see *Eight Little Piggies*, his newest book, lying on the coffee table. Dr. Gould is a unique writer. He draws subjects from popular culture to illuminate scientific concepts and lightly wraps them in humor. David Fromkin, in the *Washington Post*, comments that Dr. Gould "brings the art of the scientific essay to unparalleled heights."

Dr. Gould is also an ardent baseball fan. I highly recommend his essay "Losing the Edge" for those baseball armchair managers in the audience who have wondered why players don't have 400 averages anymore. His sales in hard and soft cover are in the millions. His writings have been translated in 15 languages, including Italian, Japanese, Spanish, French, Dutch, German, Swedish, Greek, Hebrew, Polish, Czech, and Korean. Now that is a strong worldwide voice.

The Cleveland Museum of Natural History has a long legacy of commitment to education. We were the second

* This award was presented on May 27, 1993 at The Cleveland Museum of Natural History.

science museum in the country to have an education department—and evolution plays a prominent part in the program.

I would like to mention a singular event in an Arkansas courtroom in 1981. The state of Arkansas was trying to pass a law that required the teaching of creationism in the public schools. The disciples of creationism believe that the origin of life as recounted in Genesis is literally true and that evolution is only "theory." Dr. Gould's rebuttal included the following, and I quote, "Nonsense. Evolution is as real as gravity. Whether you believe in Newton's, Einstein's, or someone else's explanation of it, the fact is that the apple still falls." As a result of his testimony, the judge threw out the law. For his role in that court battle, Dr. Gould received *Discover* magazine's 1981 Scientist of the Year award. We are deeply indebted to you, Dr. Gould, for so many reasons.

The seminal experience that set Dr. Gould's life's course was a trip to the American Museum of Natural History with his father at age five where he had his first encounter with *Tyrannosaurus rex*. Perhaps our exhibits will affect some young mind and heart in a similar way, and he or she will be the wonder scientist of the next generation — and maybe challenge your theories, Dr. Gould.

You are an inspiration to us all. You embarked on a life's search for truth in the field of evolutionary biology and have shared your conclusions through your prolific writings. Because your life has affected so many other lives, The Cleveland Museum of Natural History is pleased to confer upon you the David S. Ingalls, Jr. Award for Excellence.



Stephen Jay Gould, Museum Director J. Mary Taylor, and Norman D. Newell, just after the presentation of The Cleveland Museum of Natural History's David S. Ingalls, Jr. Award for Excellence.

A SALUTE TO STEPHEN J. GOULD

NORMAN D. NEWELL

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This is my salute to Steve. I am very pleased to be with you and feel you could not have chosen better for your first Cleveland Museum of Natural History Award for Excellence.

Our paths have not crossed often enough since we first met some 35 years ago in New York, but I have followed his career closely and I know him well. Now we are sharing the same platform. Steve would describe this meeting as a matter of chance but I think it may have been foreordained. Now I want to tell you why I think so highly of Steve in his consuming search for an understanding of life and the human condition. Let us try to imagine the rapture that overwhelmed him at five years of age when his father brought him to New York's great American Museum of Natural History. His introduction to the fearsome *Tyrannosaurus rex* was love at first sight. Neither Steve nor the dinosaur would ever again be the same, and it started Steve on a lifetime career into the history of life. Great credit is due his fine teachers at Queens PS 26 and Nathaniel Hawthorne Junior High School.

Later, as a teenager, he and schoolmate Richard Milner (who now works at the natural history museum in New York and is author of the fine *Encyclopedia of Evolution*), participated in science fairs to exhibit and broaden their knowledge of fossils. Remember, this was long before the modern fashion of representing dinosaurs on ties, T-shirts, and picture books for kiddies. In fact, few people outside New York and a few other major cities knew much about dinosaurs. I like to imagine that Steve and Richard started the ball rolling in their generation.

During this period they were frequent visitors to the natural history museum, which had the greatest exhibition of dinosaurs in the world. Steve became thrilled with a vision of nature so unlike his big city, and was challenged by the concept of organic evolution.

I first met him when, as a schoolboy, he came to do some research in my laboratory at the Museum. This seemed normal to me because my own father had introduced me at the age of 10 to the romance of the history of life.

Steve's early interest in the philosophy of science was enhanced by his studies at Antioch College where he obtained his A.B. degree. He later returned to New York for the Ph.D. at Columbia University, and studied evolutionary

biology and paleontology with experts at the American Museum. Steve honors me by calling me his teacher, but my role was primarily to encourage him and to point out promising opportunities. The communication between us was an interchange with mutual benefits, and I continue to learn from his steady stream of publications.

At Harvard University, where he teaches biology, geology, and the history of science, he is exceedingly popular with his regularly oversubscribed classes.

When I asked a neighbor, who had been a humanities student at Harvard some years ago, for his reminiscences, he wrote me the following: "My lecture course with Steve Gould in my freshman year was one of the two or three intellectually most exciting experiences during my entire stay at Harvard (and remember 400 people attended this lecture course; it was not a small intimate discussion group as were the other high points). I can still remember anticipating his lectures with real eagerness."

Steve is both humanist and scientist. As any reader of his *Natural History* magazine columns will know, baseball is his favorite sport and he regularly sings baritone with the Boston Cecilia Choral Group.

His fame extends far beyond the classroom. In abundant broadcasts, publications and popular lectures he fashions a coherent and rational view of the pathways of past and present life. His contributions range through planetary, geological, biological, and social sciences as well as political history, but they are always united by the common thread of evolutionary theory. His works bear such piquant titles as *An Urchin in the Storm*, *The Panda's Thumb* and *Eight Little Piggies*.

Currently, at a time of generally low scientific knowledge, when human distress is spreading over the Earth with the exponential growth of population, Steve is a calming voice of reason. And I believe that the population explosion is the basic cause of much of the world's misery. With homely metaphors and whimsical humor he corrects popular misconceptions about the world in terms that are both entertaining and understandable even to the non-scientist. He does not exaggerate or trivialize scientific concepts.

His prose is friendly, sprinkled with anecdotal asides, and he likes to build from tangential details to broad generalities. He has a gift for startling comments in the service of

his explanations. For example, "My cat may manipulate my psychology, but he'll never play the piano or type a letter."

As a measure of his influence and the public appreciation of his gift, 81 institutions over the world have honored him with their highest awards. These include 34 honorary doctorates of science, humanities and law, an additional 12 literary, and 36 other academic honors.

Besides invited lectures and university teaching, Steve's medium of communication has been popular writing, especially a lively and entertaining monthly article, "This View of Life," in *Natural History* magazine — 209 issues to date. These have been collected in a dozen or so books which have been highly praised by scientific and literary critics.

Fine examples of his extraordinary range and skill are two beautiful coffee table volumes written with celebrated photographer Rosamund Wolff Purcell. These are devoted to historically significant museum collections of artifacts and natural history specimens other than fossils.

His important technical publications, on the other hand, include a large tome on the biological significance of growth changes in animals (*Ontogeny and Phylogeny*) and numerous papers, based on his many days of fieldwork on the mechanics of species splitting in a tropical land snail.

General evolution has occupied much of Steve Gould's career. In my brief comments what can I say? Steve succinctly explains complex scientific principles to general readers. As mechanisms of evolution, he stresses the complex interplay of chance mutations, variability, isolation, natural selection, contingency, and extinction.

He explains the development of ideas since the early days of Linnaeus, Lamarck, Hutton, Lyell and Darwin — leading to our current success in reading the layered crust of the Earth like a history book.

His handling of the history of changing ideas about evolution is informative, leading to Darwin's careful marshalling of evidence and demonstration that evolution has neither purpose nor goal, but results from biological and physical causes.

While reading some of his writings recently, I have been impressed by the way he handles the controversial subject of discontinuities between groups of organisms and fossil sequences. He includes both physical and biological causes for gaps in the stratigraphic record. Some of the greatest gaps correspond to global episodes of mass extinction, suggesting a kind of catastrophism based on natural rather than supernatural causes. The scientific evidence suggests marked climatic and geographic changes and impacts with comets.

The fossil record shows a long succession of bursts of speciation in individual branches, alternating with intervals of stability. In 1972, Niles Eldredge of the American Museum, working with Steve, published on interruptions in the record, calling the phenomenon "punctuated equilibrium." They showed that the stable intervals displayed hardly

any recognizable changes, a condition they called "stasis." Their theory builds on work by Darwin and Ernst Mayr, the great Harvard biologist.

The crucial observation is that changes in organisms are most rapid in small, isolated populations. Islands are notable for generating their own faunas and floras in isolation. According to Eldredge and Gould, the split of a new species from an old one under natural conditions may require a few hundred years. This seems almost instantaneous in geologic time — the "punctuations" of evolution. The speciation event is followed in most, but not all cases, by stasis for millions of years before the organism becomes extinct.

Thus, there is relatively little change within species after initial speciation. Evolutionary trends and higher categories result from a sorting among more and less successful species, and not as a process occurring within single populations. The result is not the conventional tree of life with a central trunk, but a bush of life with radiating limbs and twigs.

After much profitable controversy about this theory, accumulating evidence has produced a favorable consensus. Stasis is easily documented in the fossil record but the "punctuations" are not readily distinguished from non-biological gaps.

Steve is attracted to major issues that require exploration and integration of diverse approaches. These are interdisciplinary exercises which invariably involve differences that can touch the emotions. After all, scientists are human. However, the resulting debates are salutary, and this is the way science advances.

In *Time's Arrow, Time's Cycle*, Gould shows how fossils provide evidence of genealogies. For example, a major group of marine reptiles, the ichthyosaurs, became extinct 75 million years ago. Evidently they were descendants of land dwelling reptiles that returned to the sea. Ichthyosaurs evolved a most uncanny resemblance to fishes, developing a dorsal fin in the proper hydrodynamic position, and a tail fin with two symmetrical lobes. But the ichthyosaurs still retained fundamental signs of their reptilian heritage.

The dorsal fin does not contain the bony supports found in fishes; the vertebral column bends into the lower lobe of the tail, not into the upper, as in fishes; the supports of the flippers are finger bones, not fin rays. In other words, this design was an adaptation to a particular environment. The fish shape is a common adaptation of good design, also seen in mammals such as whales.

Another of Steve's books, a charming one called *Wonderful Life*, deals with early life and its bearing on humanity. Intensive ongoing searches in Precambrian rocks show that already diverse one-celled organisms existed on Earth at least 3.5 billion years ago. Many-celled plants and animals did not appear until after more than three-quarters of the known history of life. An inference from this long delay is that, while simple life on Earth may have been

inevitable, complex life was not. There is a lesson here for seekers of intelligent civilizations elsewhere in the universe!

He tells of a remarkable assemblage of fossil marine animals more than one-half billion years old in the Canadian Rockies (the Cambrian Burgess Shale fauna). Most of the fossils are unlike any other animals known to science. They arose from unknown ancestors and shortly became extinct without descendants, save for a primitive shrimplike form and a wormlike animal with a basic anatomical feature that allies it with the major animal division to which we belong (Chordata).

Steve cites this unique assemblage of animals as an example of the chaotic events of evolution, whose details are chancy and contingent on preceding events. There is no obvious explanation why a tiny wormlike creature, our own probable ancestor, should have survived while most of the odd types disappeared without descendants. This was evidently an early experiment that failed, probably because of some environmental accident. Had conditions been slightly different and the Burgess "worm" had died out with the others, we, you and I, would never have appeared.

Another of Steve's eyeopeners concerns the long association of dinosaurs and mammals, for 135 million years, through most of the Mesozoic Era. The diverse mammals of that time were very small, inoffensive creatures that could not compete effectively with the dinosaurs that had preempted almost every ecological niche. Immediately after the mass extinction of the dinosaurs, the mammals underwent a major radiation eventually leading to our own lineage. Clearly, they had been repressed by the dinosaurs. From this we may infer that we owe our very existence to the disappearance of the dinosaurs.

Scientists must, of course, be morally responsible; and Steve has always been deeply concerned with the immorality of prejudice, especially racial prejudice. This prompted his study of IQ intelligence tests. In 1912, H. H. Goddard was the popularizer of the IQ scale, which he considered to be an accurate measure of innate intelligence. He graded people by traits which he thought were inheritable, arguing that underprivileged people were usually low on the scale because of inferior intelligence. This pernicious idea is still prevalent.

In 1969 William Jensen expanded the notion to cover inferior and superior genes and made it a public issue. Compensatory education failed, he said, because the black children it attempts to aid are genetically inferior in intelligence to white children. Steve brings biological principles to bear on this problem. He points out that modern geneticists consider variation within and between groups as two entirely different phenomena. The differences in IQ between groups have complex causes, mainly because of differences in environmental opportunities. On the other hand, there are usually significant genetical differences between individuals within single family groups.

Skills are acquired by training, not by inheritance. Black and brown people achieve high attainments in all fields: the arts, government, athletics, etc., wherever opportunities permit. In his book, *An Urchin in the Storm*, Steve maintains that as long as teachers and national leaders act upon the belief that intelligence is fixed in particular genes, human potentials will be sacrificed.

Stephen J. Gould is a great educator, attracted by issues that require research and integration; he is profound in his exploration and tries to be fair in his treatment of opponents. Behind that friendly cherubic countenance, however, there is a sleeping tiger. It was inevitable for him to lead in challenging the anti-intellectual politics of the religious right. This is not a new problem. In 1896, Andrew Dickson White, president of Cornell University, published a two-volume work, *Warfare of Science with Theology*.

Steve quotes White, a devout Christian, about the conflict: "Interference with science in the supposed interest of religion, no matter how conscientious such interference may have been, has resulted in the direst evils both to religion and to science; on the other hand, all untrammelled scientific investigation, no matter how dangerous to religion some of its stages seemed to have been, has invariably resulted in the highest good both for religion and for science" (White, 1896, p. viii). Let me stress, this was written in 1896, at the height of an anti-Darwinian furor.

In the 1920s, the previously quiet fundamentalist movement abruptly became an aggressive evangelistic crusade. It was based on the fear that children were being taught to deny God and the Bible, reject family values, and fashion their morality on what they called "Social Darwinism." In many states, statutes were enacted to prohibit the teaching of organic evolution in the schools or, as a compromise, to give equal attention to biblical creation whenever evolution was discussed.

Many years passed before these state laws were struck down by district courts, with Steve's help. Finally, in 1987, the Supreme Court decreed that "creation science" is not science. This ruling, however, turned out to be only a minor victory for science.

Fundamentalists have their own schools where they are free to stress biblical creation as literal truth in every detail. They have, more recently, become an organized political power supporting their own candidates for public office.

Steve feels religion has the supreme mission of promoting morality, ethics and the Golden Rule. However, judgments about biology, geology, and scientific cosmology require special knowledge not possessed by most theologians. His ire is aroused by attacks on science education by the religious right. Knowing the Bible well, he effectively and firmly refutes their narrow interpretations.

Steve Gould enjoys dissecting and challenging dogma and outmoded concepts in the interest of truth. In debates, he is confronted by vernacular use of some common words

such as "facts," "truth," "evidence," "theory" and "proof," all of which frequently mean different things to scientists and laymen. He is careful to define his terms.

The word "theory" is an example. It has two meanings. To the general public it usually means something that is speculative; to the scientist it is a concept based on firm evidence. The theory of evolution is based on verifiable observations. The so-called "theory of special creation" has no objective support. It is a hypothesis, a belief or fantasy.

Gallup Polls in 1987 and 1992 reported that almost one-half of the United States population believes in a universe created miraculously only a few thousand years ago, and tenanted only by the living species that survived Noah's flood.

The literal belief in the book of Genesis now commands a growing audience greater than at any time since Darwin. At prime time one February evening, CBS television showed a two-hour documentary film describing the "amazing discovery of the Ark on Mount Ararat." I wonder if any of you saw it? It was certainly no credit to CBS!

It is our way to be suspicious of changes that challenge our beliefs. For more than four generations, millions of poorly informed religious conservatives have regarded Darwinism and evolution as an evil threat to their faith and to their way of life. But in spite of their spokesmen, evolution is, indeed, a fact. It is a tragedy that they choose peace of mind over the scientific truth.

Why do people find evolution uncomfortable? Carl Sagan has put this well when he asks if we should accept a comfortable lie, or embrace the uncomfortable truth. I was nonplussed to be told not long ago, at the end of a general lecture on evolution, "I don't care if what you say is true, I don't wish to believe it. I find comfort in my religion, not from science."

Widespread public ignorance of the historical sciences of biology, geology and astronomy fuels fundamentalism. As Gould says in *Wonderful Life*: "History, with its quirky pathways and quixotic reorganizations teaches a hard lesson. Unless God is even more inscrutable than we ever dared to imagine (or unless He explicitly designed our modes of thought so that we would never grasp His own), the history of life confers no special or preordered status on human intelligence. Life's history is massively contingent — usually dependent — on particulars of history, quite unpredictable and unrepeatable. They divert futures into new channels, shallow and adjacent to old pathways at first (like the twigs of a bush), but deepening and diverging with the passage of time.

"If we could play the game of life again, history would roll down another set of utterly different but equally explainable channels. If life's history cannot be read as an ascending ladder to human wisdom, step after predictable step, neither can the opposite pole of true randomness capture its evident order." In other words, if there is any biological order in nature, it is based on both natural selection and chance, not on plan and purpose.

Steve straightens out popular misconceptions, and helps the non-scientist understand the historical sciences and how nature works. If everyone down through history had lacked curiosity about the universe, there would be no basic science, no technology, no heavy industry, no medicine, and we would be living in caves with population numbers of only a few million rather than the present teeming billions.

We are here tonight to celebrate the gifts of an extraordinarily talented individual of strong motivations and great stamina. He has influenced very many people, students and general public alike, through his life and his work. His enthusiasm is infectious, and his remarkable ability to teach and express himself are rare qualities to be treasured.

Stephen J. Gould, our thanks and congratulations. But remember, at your mid-career, there is still much work for you to do!

Books by Stephen Jay Gould

(Published by W. W. Norton & Company, New York and London, unless otherwise noted.)

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REPLY

STEPHEN JAY GOULD

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Cambridge, MA 02138*

I have dedicated two of my books to teachers. One of my most recent, *Wonderful Life*, honors the man who introduced me tonight: "To Norman D. Newell, who was, and is, in the most noble word of all human speech, my teacher. (I conducted a little internal debate between "parent" and "teacher" for the designation of "most noble word," but decided on the latter as a relationship of choice rather than, at least in one direction, necessity.) One of my earliest books, *The Panda's Thumb*, honors three of my primary school teachers with a quote from Henry Adams: "A teacher... can never tell where his influence stops."

Did you have any inkling, Norman, when you received that bratty letter from a teenaged kid looking for a Westinghouse science project for the high school fair, that both of us, as members of the AARP nearly forty years later, would be celebrating so many years of mentorship and collegiality? A teacher can never tell where his influence stops. *Verbum dei manet in aeternum. Deus* (God) is *dominus* (lord); *dominus* (lord) is don (teacher). So the line does apply to you, and you shall always be the strongest influence upon my professional life. For that precious gift, there are no words — except to acknowledge you as my teacher.

But the happy coincidence of your presence in one of the nation's great natural history museums does allow me to make a crucial point about our common calling, and our commitment to the study of life and its history. Diversity is nature's distinctive calling card — her pervasive empirical theme and the result of the principles (natural selection and other components of evolutionary theory) that regulate life's history. Vicarious and virtual illustrations have their limits. Pictures and flashing lights may capture our fancy, but only authentic objects of nature can fully stir both our souls and our intellects. The natural history museum — with its focus on collecting and displaying life's rich diversity — must therefore be the institution of choice for students of this most fascinating of all biological subjects.

Yet, we all feel an ebbing of support from both public and professional domains — professional, as academic biology moves ever so strongly to a molecular beat (so far so good) and tragically casts aside (now becoming bad in lamentable shortsightedness) the study of whole organisms as a superannuated mode of inquiry; and public, as the glitz of "theme park" museums (and their contentless gift-shop



Stephen Jay Gould grasping the bronze sculpture given as a symbol of the David S. Ingalls, Jr. Award for Excellence. The sculpture, "Kneedeep," was a playful attempt by sculptor and Museum assistant director Laurence G. Isard to capture a moment of awkward grace in a frog's attempt to reach new heights.

paraphernalia) threaten to beat the substance of nature's real objects into a secondary and neglected status.

We must fight back, and the battle is far from hopeless. Disney's forthcoming history theme park in Virginia may draw more people than the Gettysburg battle site, but Gettysburg remains thronged with passionately fascinated people. Natural history museums need not outcompete MTV; they simply must be chock full of people who love science and the living world — and such people exist in more than adequate numbers.

I focus upon the conjunction of Norman Newell, a great museum paleontologist, with The Cleveland Museum of Natural History, a grand museum of its genre, because these two facets of our shared professional life represent what we must retain if we are to survive with integrity. Great museums must be places of active research, not merely static display. If the public exhibits are the entirety, and not the tip of an iceberg formed by study specimens in drawers, material just collected and ready for cataloguing, and, above all, the hum of curators and researchers engaged in formulating new knowledge about natural history, then the institution will have no dynamic foundation, and will eventually die. The public often doesn't even know that research and publication form the backbone of all great museums — and we should advertise this function more openly, and with pride. Norman Newell, one of the world's greatest paleontologists,

has spent his career at the American Museum of Natural History in New York. He stands for the best of this too invisible tradition.

The Cleveland Museum represents one of a diminishing number of great institutions — New York, Harvard, Yale, Chicago, Philadelphia, Pittsburgh, and San Francisco also come prominently to mind — committed to the old ideal of displaying nature's diversity through stunning and instructive specimens. There will never be any substitute for authenticity, no matter how close virtual reality comes to the actual, and no matter how exciting the lights and motion of theme parks can become. So long as real objects continue to stir us, our humanity will be intact and our ties to the earth that made and nurtured us will prosper. Long may the great museums of nature's diversity flourish.

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The Cleveland Museum of Natural History

February 1996

Number 49: 1-5

BLASTOIDS FROM THE CUYAHOGA FORMATION OF OHIO (ECHINODERMATA; LOWER MISSISSIPPIAN)

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ABSTRACT

Blastoid echinoderm fossils are reported for the first time from the Lower Mississippian Cuyahoga Formation of northern Ohio. Although two species are present, poor preservation prevents specific and generic identification. Regardless, this is an important occurrence because few blastoids are known from the Kinderhookian-early Osagean siliciclastic environments represented by the Cuyahoga Formation.

Introduction

Five blastoid specimens, perhaps belonging to two new species, have recently become available from Lower Mississippian strata of northern Ohio. Although a diverse crinoid fauna has been known from the Lower Mississippian Cuyahoga Formation since the monographic works of James Hall (Hall, 1863; Hall and Whitfield, 1875), blastoids have never been reported from these strata.

The precise age of the Cuyahoga Formation has been equivocal, largely because of a lack of biostratigraphically diagnostic fossils. Apparently, it was deposited sometime between the late Kinderhookian and middle Osagean (Szmuc, 1959; Hoare, 1990), and the Kinderhookian-Osagean boundary probably lies within the Cuyahoga. Recently, Carter (1985) indicated that Cuyahoga Formation brachiopods have strong Kinderhookian affinities, but Gordon (1986) reported early Osagean ammonoids in the upper part of the Cuyahoga Formation.

This small, poorly preserved blastoid fauna is significant, regardless of its Early Mississippian age. Relatively few blastoids are known from the late Kinderhookian-early Osagean interval, the more probable age of the Cuyahoga Formation, especially in the midcontinent. So despite the poor preservation, recognition of the presence and facies occurrences of these blastoids is quite important. If these new blastoids are slightly younger, middle Osagean and contemporaneous with the Burlington Limestone, this occurrence would also be significant by demonstrating that both fissiculate and granatocrinid blastoids were present in shallow water siliciclastic environments during the middle Osagean, even though this was not an optimum habitat.

Blastoid abundance and diversity reached its historic high in the Burlington Limestone. Approximately 17 blastoid genera are recognized from the Burlington Limestone, and blastoids are one of the more common fossils in that unit. The Burlington is characteristic of middle Osagean and Early Mississippian blastoids, because they typically are most common in carbonate environments (Waters et al., 1982; Sprinkle and Gutschick, 1990). At the close of the middle Osagean, a major extinction event occurred among blastoids (Ausich et al., 1988). Immediately following that extinction, blastoids were no longer common and diverse in shallow-water carbonate environments such as the Burlington Limestone. Instead, they were better represented in basinal siliciclastic or mixed siliciclastic/carbonate facies such as the New Providence Shale Member of the Borden Formation or the Fort Payne Formation (Ausich et al., 1988; Ausich and Meyer, 1988). Further study of Cuyahoga Formation blastoids from Ohio and other coeval blastoids from siliciclastic facies may reveal the ancestral roots of the late Osagean basinal blastoid faunas. Did the younger blastoids evolve from among the blastoids from carbonate environments such as the Burlington Limestone or from blastoids in siliciclastic environments such as these reported here from the Cuyahoga Formation?

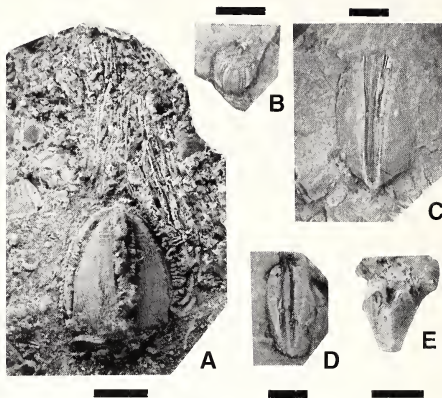


Figure 1. Photographs of Early Mississippian blastoids from Ohio. A-D, granatocrinid gen. and sp. indet.; A, latex mold of a nearly complete specimen in lateral view, note thecal plate sculpturing and brachioles, USNM 483880; B, oblique oral view of partially crushed juvenile questionably assigned to this taxon, CMNH 5942; C, radial plate with ambulacrum in lateral view, CMNH 5942; D, very poorly preserved internal mold of a partial specimen, USNM 483881; E, *Phaenoschisma*? sp., lateral view, note that the base is partially broken away and the ambulacra are absent from the radial sinuses, USNM 483879. All bar scales equal 0.5 cm.

Two of these new blastoid specimens were collected by Guenther, one was found in the collections of the U.S. National Museum of Natural History by Ausich, and two are from The Cleveland Museum of Natural History (collected by G. Meszaros). Search for additional Cuyahoga blastoid material has been unsuccessful.

Terminology follows Beaver (1968), suprageneric classification follows Waters and Horowitz (1993) for granatocrinids and Breimer and Macurda (1972) for fissiculates, and measurements are in mm. Specimens are deposited in the U.S. National Museum of Natural History, Washington, D.C. (USNM), and in The Cleveland Museum of Natural History (CMNH).

Systematic Paleontology

Class BLASTOIDEA Say, 1825
Order FISSICULATA Jaekel, 1918
Family PHAENOSCHISMATIDAE
Etheridge and Carpenter, 1886

Genus *PHAENOSCHISMA* Etheridge and Carpenter, 1882

PHAENOSCHISMA? sp.

Figures 1E, 2A

Description

Theca small, conical in lateral view (Figures 1E, 2A), pelvis with straight sides; vault low; theca pentagonal in oval view, with interradial areas not indented; pelvic angle narrow.

Basals three, less than 50 percent thecal height (Figure 2A); one azygous and two zygous plates, basal-basal and radial-basal sutures straight; basals smooth except for growth lines parallel to radial-basal suture; proximal portion of basal circlet not preserved.

Radials five, forming more than upper half of pelvis, perhaps all of vault; radial-radial sutures straight; radial height exceeds width; interradial area straight; sculpturing smooth except for growth lines (on at least one plate) that parallel radial-basal sutures.

Deltoids not visible in lateral view; deltoid crest apparently sloping slightly downward toward the mouth.

Hydrospire slits apparently extend to abaxial margin of radial sinus (abaxial portions exposed while cleaning the sinus for the ambulacra).

Deltoids, ambulacra, hydrospires, and column unknown.

Material examined

The single specimen assigned to *Phaenoschisma*? sp. is USNM 483879.

Discussion

Specimen USNM 483879 is a partial theca preserved as a cast with an outer coating of siderite (Figure 1E). The proximal portion of the basal circlet is broken away, and the ambulacral areas are not preserved. However, plate surface details are very well preserved and still display fine growth lines (Figure 1E). The theca is small (less than 1.0 cm), is conical in shape, has a pentagonal outline in oral view, and has a vault subordinate in height to the pelvis (Figure 1E).

In general thecal shape, this blastoid appears to be similar to *Hadroblastus*, *Koryschisma*, *Pentremoblastus*, and *Phaenoschisma*. A sufficient number of morphological characters are unknown from this specimen so that positive identification is not possible. However, we can questionably assign specimen USNM 483879 to *Phaenoschisma* sp. by the process of elimination. *Hadroblastus* has wide ambulacral sinuses, a biconical calyx with the vault and pelvis nearly equal in height. *Koryschisma* is commonly larger with a longer vault and a flat deltoid crest. Specimen 483879 has relatively narrow ambulacral sinuses and a short vault in relation to the pelvis. This and the slightly downward sloping deltoid crest align this specimen with *Phaenoschisma* rather than with *Pentremoblastus*. Sprinkle and Gutschick (1990, p. 121-122) also reported an isolated *Phaenoschisma*? from the upper Lodgepole Limestone of Montana (lower

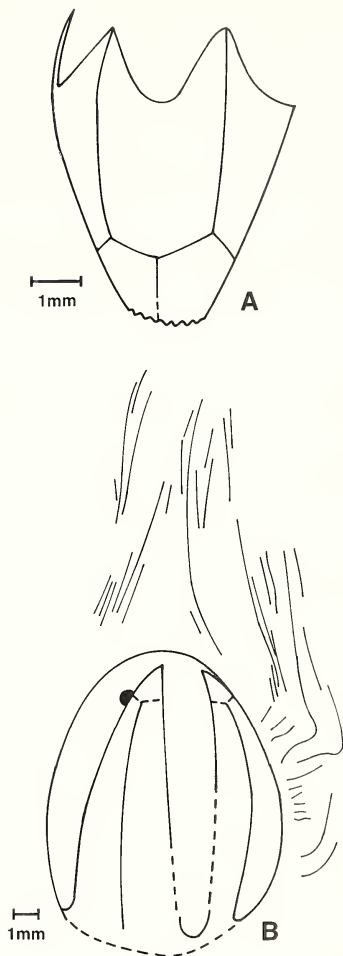


Figure 2. Camera lucida drawings of Early Mississippian blastoids. A, *Phaenoschisma*? sp., lower portion of basal circlet broken away, USNM 483879; B, granatocrinid gen. and sp. indet., USNM 483880, blackened oval is the questionable position of a spiracle, only brachiole traces are shown; dashed lines indicate uncertainty in position of plate boundary.

Osagean), but it had a shorter vault and probably a narrower theca than in USNM 483879.

Occurrence

Phaenoschisma? sp. is known from the Meadville Member of the Cuyahoga Formation along the West Fork of the East Branch of Black River. This locality is approximately 4 km (2.5 mi) east of Homerville, Medina County, Ohio. It was preserved in a siderite concretion collected from a silty limestone layer about two feet above the water level and about 4.25 m (14 ft) below the top of the outcrop.

Measurements

USNM 483879: incomplete thecal height, 6.3; maximum thecal width, 5.0; maximum basal circlet width, 2.8; radial plate height, 4.5; maximum radial plate width, 2.9.

Order GRANATOCRINIDA Bather, 1900

Family GRANATOCRINIDAE Fay, 1961

GRANATOCRINID GEN. AND SP. INDET.

Figures 1A-1D, 2B

Description

Theca medium to large size, subellipsoidal (Figures 1A, 2B); probably slightly higher than wide, widest portion near base of theca; pelvis not known but thecal shape suggestive that it may be a low cone, vault probably majority of thecal height; oral view outline rounded pentagonal; interambulacral areas slightly convex; dominant striated thecal plate sculpturing.

Basals unknown.

Radials undoubtedly five, base of radial probably quite short, limbs long, majority of thecal height (Figures 1A-1C, 2B); in oral view radials gently convex; radial sides slightly wider than ambulacral width proximally, but sides narrow distally; low ridge along the proximal boundary of radial sinus. Three sculpturing fields on each radial limb: in adambulacral-proximal position, irregular sinuous ridges oblique to the radial-radial sutures, this field narrows distally; in adambulacral-proximal position, fine straight ridges that parallel the radial-radial suture, this field expands distally; in adambulacral-distal position, straight coarse ridges perpendicular to radial-radial suture, this field thins proximally (Figures 1A-1C).

Two deltoids preserved, rhombic but nearly triangular in shape, gently convex longitudinally and along width, distal tip below peristome; sculpturing discontinuous, irregular coarse ridges approximately perpendicular to deltoid margin. Anal deltoids unknown.

Ambulacra presumably five, linear, taper in width distally, convex in cross section with groove slightly depressed, probably extend nearly to base of theca,

lancet apparently not exposed along ambulacrum.

Spiracles very poorly preserved. Regular spiracles may be ellipsoidal, situated approximately at radial-deltoid suture (Figure 2B).

Brachioles very fine, extend greater than one thecal height above peristome.

Column unknown.

Material examined

Two specimens are assigned to granatocrinid gen. and sp. indet.: USNM 483880 and CMNH 5942. Additionally, two specimens are questionably assigned to this taxon: CMNH 5854 is a juvenile and USNM 483881 is a very, very poorly preserved internal mold.

Discussion

Specimen USNM 483880 is nearly a complete blastoid with brachioles attached (Figures 1A, 2B). However, because it is preserved as an external mold of less than half of the specimen, its identity is problematic. The fidelity of the mold is excellent where present. Specimen CMNH 5942 (Figure 1C) is a partial radial plate. Detail of the plate sculpturing is excellent; and although slight differences occur between it and USNM 483830, these two specimens are considered conspecific. Long, groove-like features are present along the ambulacrum of CMNH 5942 that superficially appear to be hydrosipile slits; however, these are judged to be brachioles (complete and weathered). A second specimen from the Cleveland Museum (CMNH 5854; Figure 1B) is very small and regarded as a juvenile. It is preserved in an obliquely crushed oral orientation, and details of the summit are poorly preserved. Again, the unique details of plate sculpturing of other specimens are present on CMNH 5942, but for the present, it should be questionably assigned to this taxon. From this juvenile, the lateral position of the spiracles (Figure 2B) cannot be verified, but the spiracles are not preserved elsewhere. Another questionable specimen (Figure 1D) is a very poorly preserved, compressed specimen (USNM 483881). It is slightly more than 1.0 cm high, and it is a very poor cast in a gray shale. The only evident aspect of this specimen is the presence of long ambulacra, which probably aligns it with granatocrinid gen. and sp. indet.

Placement of the spiracles (Figure 2B) is questionable due to preservation. However, if this lateral position of the spiracles is correct, this species has 8, 9, or 10 spiracles. Specimen CMNH 5854 may have an anispiral. This along with the subellipsoidal thecal shape, relatively short deltoids, and lancets not exposed aligns this species to the Order Granatocrinida and to the Family Granatocrinidae. Because features of the basals, deltoids, and spiracles are unknown, this blastoid cannot be assigned to a genus.

Occurrence

Specimen USNM 483880 was discovered in a drawer at the U.S. National Museum of Natural History. The label accompanying this specimen has the following information "Loose Rx in stream bed Meadville fm. West Branch of Rocky R. at junction of small stream south of Abbyville, Medina Co., Ohio Coll. J.J. Happinger." Although we have been unable to recollect blastoids from this locality, this location is reasonable, and it would also have come from strata in the Meadville Member of Cuyahoga Formation.

Specimen USNM 483881 is from the Cuyahoga Formation (member not differentiated) approximately 3.2 km (2.0 mi) east of Hayesville, Ashland County, Ohio [SW¼, SW¼, SW¼, sec. 18, T21N, R16W]. Siderite concretions are also present in the Cuyahoga at this locality, but this blastoid is from a gray shale layer about 14 feet below the top of exposures at this locality. It was collected about eight inches above water level by Guenther.

Specimens CMNH 5854 and CMNH 5942 are both from the Meadville Member of the Cuyahoga Formation from an unspecified locality at or near Lodi.

Measurements

USNM 483880: incomplete thecal height, 11.8; incomplete thecal width, 9.6; maximum radial plate width, 5.7; deltoid height, 2.2; maximum deltoid width, 1.7. USNM 483881: preserved theca nearly 15 mm high; theca plus brachioles more than 30 mm high.

Acknowledgments

The authors thank William Hammer, Augustana College, Jann Thompson, U.S. National Museum of Natural History, and J. Hannibal, The Cleveland Museum of Natural History, for allowing access to study these blastoid specimens. Discussions with Alan S. Horowitz and Thomas W. Kammer were very useful, and A. S. Horowitz and J. Sprinkle improved an earlier draft of this manuscript.

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**CARYOCARIS (CRUSTACEA: PHYLLOCARIDA)
FROM THE ORDOVICIAN OF THE CORDILLERA ORIENTAL
OF SOUTHERN BOLIVIA**

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ABSTRACT

A specimen of *Caryocaris* Salter from Quebrada de Chaupiuno, northwest Tarija, Bolivia, has well-preserved posterior spinelets. The base of the carapace horn is also preserved. Examination of this specimen allows for a reinterpretation of the morphology of some previously reported specimens of the genus from South America.

Introduction

Caryocaris Salter is a widespread genus of phyllocarid, having been reported from the Ordovician of China (Shen, 1986), New Zealand (Chapman, 1934), Australia (Jell, 1980), Europe and North America (Chlupáč, 1969, p. 44; Rolfe, 1969, p. R316), as well as Peru, Argentina, and Bolivia in South America (Figure 1). *Caryocaris acuta* Bulman, 1931, found in the Ordovician of Peru, was the only South American phyllocarid noted in the comprehensive listing of Van Straelen and Schmitz (1934, *Tabulae Geographicae*, p. 212). This species has been cited a number of times and was illustrated (fig. 16, 14a) in Camacho's *Invertebrados Fósiles* (1975), published in Argentina. Ahlfeld and Braniša (1960, p. 44) were probably the first authors to note the presence of *Caryocaris* in Argentina, however. They reported *Caryocaris* sp. from the Río Toro area, south of La Quiaca, in the "Arenigian" of northern Argentina. Later, Aceñolaza et al. (1976) described and illustrated specimens of *Caryocaris* from the "Arenigian" of the La Alumbra River region, Catamarca Province, northwest Argentina. They also noted the occurrence of the genus in the Acote Formation of Sierra de Cajas, Jujuy Province, northwest Argentina. Ramos (1984), in the most comprehensive paper on Argentinian caryocaridids to date, reviewed most occurrences in that country, corrected misidentifications, and provided a locality map showing their distribution. He also described and illustrated specimens of *Caryocaris* from Piscuno sur, Departamento La Poma, northwest Argentina. Several Bolivian occurrences of *Caryocaris* have been noted by Suárez-Soruco (1976, fig. 26) and Hughes (1980, table 1), who reported *Caryocaris* sp. as occurring in Tremadoc and Arenig faunas, and *Caryocaris acuta* Bulman as occurring in Llanvir/Llandeilo faunas.

The purpose of this note is to describe a specimen of *Caryocaris* (Hunterian Museum GLAHM 101139) from Bolivia and to briefly comment on other, previously described material from South America. Description of the well-preserved Bolivian specimen makes it possible to reinterpret the fossils previously reported from Argentina.

According to L. Braniša (personal communication to W. D. I. Rolfe), the Bolivian specimen is from Quebrada de Chaupiuno, northwest Tarija, near the junction of the Río San Juan and Río Pilaya (Figure 1, locality 2). It is preserved on a small slab of dark gray siltstone. The specimen is part of a small assemblage, now housed at the Hunterian Museum of Scotland, from the Quebrada de Chaupiuno locality. This assemblage also includes at least one other small slab containing phyllocarid specimens, possibly *Caryocaris*, but the additional material is fragmentary and poorly preserved. Other specimens in this assemblage are preserved in shales that range in color from pale yellowish brown to medium gray to mottled brownish grey and pale red.

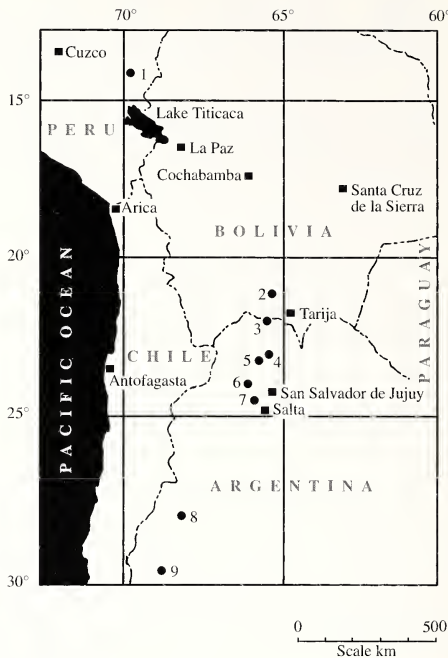
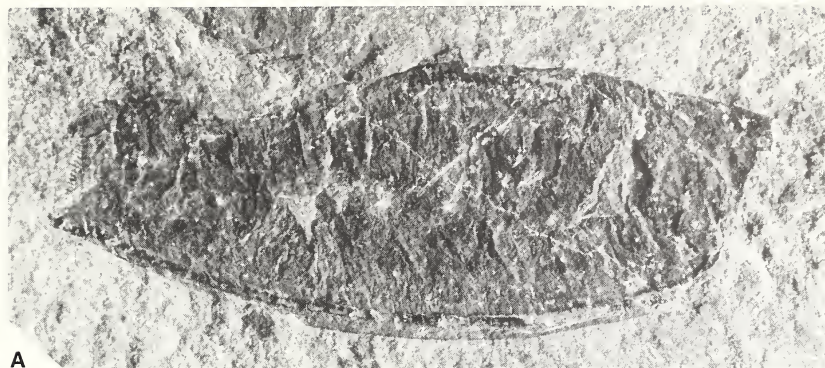
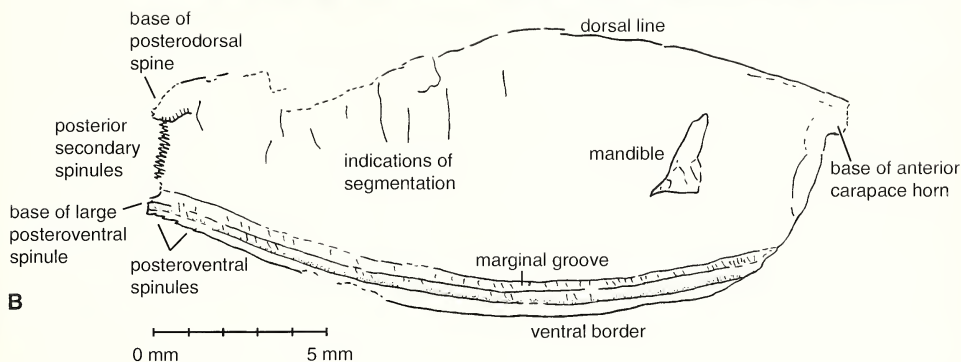


Figure 1. Locality map showing occurrences of *Caryocaris* in South America. 1, Huichiyuni, Peru (Bulman, 1931); 2, Quebrada de Chaupiuno, Bolivia (this paper); 3, Río Toro area, south of La Quiaca, Argentina (Alfeld and Braniša, 1960); 4, Sierra de Cajas, Argentina (localities 4-9 after Ramos, 1984, which contains additional data and references on these occurrences); 5, Sierra de Aguilar, Argentina; 6, Piscuno sur, Argentina; 7, Puerta de Tastil, Argentina; 8, Río La Alumbra, Argentina; 9, Río Gualcamayo, Argentina.

Because the specimen of *Caryocaris* was collected in the same horizon as the graptolite *Tetraraptus quadrirachiatius* (Hall), it was assigned to the Lower Ordovician (Arenig) by L. Braniša (personal communication to W.D.I. Rolfe, 1962; see also Alfeld and Braniša, 1960, fig. 14). Aceñolaza et al. (1976) also assigned a fauna containing *T. quadrirachiatius* and *Caryocaris* to the Arenig. The distribution of *T. quadrirachiatius*, however, may extend into the Llanvirnian (Aceñolaza and Durand, 1975). Rivas et al. (1969) have described the stratigraphy of the Ordovician of the Tarija area, and have provided a stratigraphic section of the rocks of that area.



A



B

Geologic mapping done just to the south of the Bolivian locality (Pacheco et al., 1991) indicates that the *Caryocaris* specimen probably came from the Pircancha Formation, which is, at least in part, Llanvirnian.

Systematic Paleontology

Superorder PHYLLOCARIDA Packard, 1879

Order ARCHAEOSTACA Claus, 1888

Suborder CERATIOCARINA Clarke in Zittel, 1900

Family CERATIOCARIDIDAE Salter, 1860

Genus *CARYOCARIS* Salter, 1863

CARYOCARIS sp.

Figures 2-3

Description

Carapace 20.8 mm long, elongate, average size for genus. Dorsal line moderately convex, maximum valve width 7.9 mm, with greatest width just anterior to midlength. Width of posterior less than that of anterior.

Figure 2. *Caryocaris* sp., Hunterian Museum GLAHM 101139, from Bolivia. A, Entire specimen, scale bar = 1 mm; B, Camera lucida drawing of specimen.

Anterodorsal corner produced into base of carapace horn. Anterior margin probably convex. Curved thin groove delineates lunate area adjacent to anterior margin. Ventral margin smoothly and moderately convex. Ventral border wide, with strong, rounded, centrally located ventral ridge separated from carapace by shallow marginal groove (border line). Ridge and groove marked by posterodorsally oriented ornamentation. Ventral border smooth, except for several posteriorly directed, very fine spinules located toward posterior. Posterior margin straight, inclined slightly dorsad, terminating with many short, closely spaced (about nine per mm), posteriorly directed secondary spinules. Posterodorsal and posteroventral corners of carapace produced as bases of posterodorsal spine and large posteroventral spinule.

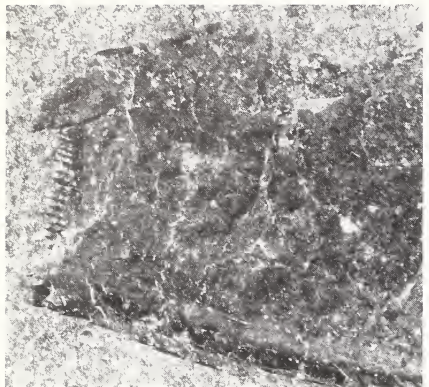


Figure 3. *Caryocaris* sp., Hunterian Museum GLAHM 101139, from Bolivia, close-up of posterior of carapace, showing posterior spinules, scale bar = 1 mm.

Remarks

This specimen probably represents most of the carapace, with the left side folded beneath the right. Most of the exposed part of the specimen is part of the right valve, but in places, for instance along part of the posterior margin, the right valve seems to be broken away, exposing portions of the left valve. This is indicated by a drop, denoted by hachures on Figure 2B, from one layer to another near the posterodorsal corner. Part of the left valve may also be exposed along the anterior margin. It is also possible that the ventral border as interpreted here includes some overlapping parts of both the right and left valve. Most of the carapace is finely and irregularly wrinkled, probably due to taphonomic processes.

The impression of a mandible is preserved toward the anterior of the specimen. This impression shows that the mandible of *Caryocaris* is average sized for a phyllocarid. Transverse markings, approximately equally spaced, in the posterodorsal portion of the carapace provide some indication of thoracic and/or abdominal segmentation impressed through the carapace.

The overall shape of this specimen, coupled with the presence of posterior spinules (Chlupáč, 1969) permits confident placement of this specimen in the genus *Caryocaris*. Comparison of this specimen to other described specimens is hampered, however, by our imperfect knowledge of the morphology of previously described caryocaridids from South America including the Upper Ordovician *Caryocaris acuta*, from Huichiyuni (near Limpucuni), northwest Peru (Bulman, 1931); *Caryocaris* sp. from the Acoite Formation of Argentina (Aceñolaza et

al., 1976); and *Caryocaris* sp. from Piscuno sur, Departamento La Poma, Provincia de Salta, Argentina (Ramos, 1984). The Bolivian specimen described here, with a width-to-length ratio of 1:2.7, is less elongate than is *C. acuta*, which, based on Bulman's average measurements, has a width-to-length ratio of 1:3.5. However, this average figure may be skewed by the inclusion of specimens that may be partially enrolled. The very elongate shape of the Peruvian specimen figured by Bulman (1931, pl. xi, fig. 7) suggests enrollment of the holotype. The Bolivian specimen appears to have a more curved dorsum than does the holotype of *C. acuta*, but this could be due to enrollment of the latter specimen. Also, the nature of the posterior of *C. acuta* is not known, hampering comparison.

The overall shape of the carapace of the Bolivian specimen is similar to that of at least some of the specimens from Argentina described and illustrated by Ramos (1984). The length-to-width ratio of the carapace of the Bolivian specimen is also similar to the large specimens described by Ramos. Upon first inspection, however, the Bolivian specimen seems to differ in several ways from the specimen reconstructed by Ramos (1984, fig. 2). Examination of the well-preserved Bolivian specimen suggests a revision of the interpretation of some of the Argentinean material. The "posterior" of the carapace of some illustrated specimens (Ramos, 1984, Pl. 1, at least those specimens seen in figs. a & b) is actually the anterior. The anterior of the carapace of Ramos's reconstruction (fig. 2) is the posterior. This necessitates changing of the position of the telson and abdomen to the other side of the carapace as illustrated. With these changes, this reconstruction more closely resembles the specimen illustrated herein as well as other described specimens of *Caryocaris*.

The apparent lack of carapace spinules, as well as carapace horns, on various previously described specimens of the genus from South America may well be due to poor preservation. If this is so, it argues for the synonymy of *Rhinopterocaris* and *Caryocaris* suggested by Rolfe (p. 183 in Theokritoff, 1964; 1969, p. R316; 1981, p. 23). These two taxa were distinguished by the presence or absence of carapace spinules and produced carapace horns.

Caryocaris has often, but not always (Churkin, 1966, p. 377), been found in association with, or in the same layers of strata as, graptolites (Rolfe, 1969, p. R307; Bassett and Berg-Madsen, 1993; Chlupáč, 1969, pp. 66). In fact, Gurley (1896, p. 86-88) described caryocaridids as graptolites! The Bolivian occurrence reported here is like most previous occurrences as far as age and association with graptolites is concerned. The similarity of the carapace of *Caryocaris* to parts of various graptolites, coupled with the presumably close physical relationship of *Caryocaris* to various graptolites as part of Ordovician plankton, has been suggested to be the result of mimicry.

Acknowledgements

Leonard Braniša, through a letter to W. D. I. Rolfe, provided stratigraphic information on this and other specimens from the Ordovician of Bolivia. He also donated the specimen to the Hunterian Museum. Loan of the specimen was kindly provided by W. D. Ian Rolfe, Royal Scottish Museum, who also first identified *Caryocaris* from the suite of material donated by Braniša. LeGrand Smith, Yorktown, Virginia and Herberto Perez G., Servicio Geológico de Bolivia, helped us obtain geologic maps of Bolivia and Neil D. L. Clark, Hunterian Museum, provided advice on stratigraphic and other matters. Bruce Frumker, The Cleveland Museum of Natural History, took the photographs used in this article. This paper was improved by helpful reviews by Rolfe and by Murray J. Copeland, Geological Survey of Canada. Contribution 567, Department of Geology, Kent State University, Kent OH 44242.

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ORGANIC MATRIX COMPOSITION OF MODERN AND 8.7K BP *MYA TRUNCATA* (MOLLUSCA: BIVALVIA) FROM ARCTIC CANADA

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ABSTRACT

Amino acid and amino sugar compositions of the organic matrices of modern and subfossil *Mya truncata* shells from Arctic Canada were determined by high-performance liquid chromatography analyses. Comparison of compositions of modern and subfossil hydrolyzed soluble and insoluble matrix residues reveals that modern and 8.7k BP samples show statistically significant differences resulting from post-mortem alteration. These findings suggest the potential geochronological usefulness of matrix residues from *M. truncata* subfossil shells. Nevertheless, post-mortem hydrolysis of the insoluble matrix likely contributes to the composition of the soluble fraction collected from subfossil shells. This process hampers defining the true composition of the subfossil soluble matrix and inferring soluble matrix diagenesis.

Introduction

Mollusk shells contain a small amount ($\leq 5\%$ by weight) of organic matter called an organic matrix. This matrix is divided into soluble or insoluble components depending on its behavior in decalcifying media and acids. The matrix is both an agent and a product of biomineralization processes (Lowenstam and Weiner, 1989).

One or two amino acids, usually glycine or glycine and alanine, are the principal monomeric components of mollusk insoluble matrices. These and other amino acids function as monomeric constituents of hydrophobic proteins (Meenakshi et al., 1971; Grégoire, 1972). Amino sugars, such as galactosamine and particularly glucosamine, are also important parts of the insoluble matrix of many species. Glucosamine is the monomeric constituent of chitin, which is located between protein sheets (Goffinet and Jeuniaux, 1969; Weiner and Traub, 1980). Other matrix carbohydrate monomers include the monosaccharides altrose, fucose, galactose, glucose, mannose, and xylose, which have been identified in the form of silylated derivatives. The role of some of these and other carbohydrates in the matrix may be as carbohydrate constituents of glycoproteins (Tevsz et al., 1992; 1994).

Sulfated glycoproteins comprise a major portion of the soluble matrix (Simkiss, 1965; Crenshaw, 1972). These proteins are rich in aspartic acid and can bind calcium ions. The two fractions of the organic matrix come from two different sources within the shell. The insoluble matrix is mainly located between crystals of calcite or aragonite, while the soluble matrix has an important intracrystalline component.

The geological use of information from organic matrices began when Ableson (1954) reported the occurrence of amino acids in fossils. Subsequent investigations have focused on the source, distribution, composition, and diagenesis of matrix constituents. An important geological use of information from insoluble matrix has been as a source of absolute ages and as biostratigraphic correlation tools. This work is based on time-related changes in ratios of matrix amino acids and also the extent to which certain amino acids have undergone racemization (Wehmiller, 1990; 1993).

Because the soluble component of the organic matrix has an intracrystalline component, some workers consider it to be more resistant to diagenetic change than the more "exposed" insoluble matrix. Thus, it has not been used as much for chronological work as has insoluble matrix but has proven useful as a source of information for taxonomic and phylogenetic studies (Muyzer et al., 1988; Lowenstam and Weiner, 1989; Robbins et al., 1993).

This paper describes and compares for the first time amino acid and amino sugar compositions of the organic matrices of modern and subfossil *Mya truncata* Linnaeus, 1758 (Mollusca: Bivalvia) from Arctic

Canada. New data are presented on the soluble fraction and comparisons are made which involve existing insoluble fraction data. In order to facilitate comparisons, we have focused our attention on the most abundant and easily detected amino acids and amino sugars. We describe differences resulting from post-mortem alteration of soluble and insoluble matrix fractions of modern and subfossil shells and comment on the potential geological usefulness of this information.

Mya truncata is an abundant modern marine bivalve and is also common and widespread in Pleistocene and Holocene marine deposits throughout northeastern North America (Aitken, 1987; Aitken and Risk, 1988). The modern specimens for this study were collected alive within a few meters of the subfossil shells, which obviates the possibility of compositional differences between modern and subfossil samples being caused by the sample sets being drawn from geographically distant populations. It is assumed that the 8700 year interval separating the modern and subfossil populations was too brief to permit significant evolutionary changes to occur in the proportions of monomeric constituents of the organic matrix. Thus, compositional differences between subfossil and modern samples likely reflect *in situ* changes occurring to the matrix within the measured time interval. Because the subfossil specimens collected for this study were from localities in high latitudes, post-mortem matrix alteration was likely minimized because of the low temperatures to which the shells were exposed (Risk, 1991).

Materials and Methods

Well-preserved subfossil shells of *Mya truncata* were collected from raised beaches at Pangnirtung Fiord, Baffin Island, Northwest Territories, Canada ($66^{\circ} 08' \text{ N}$, $65^{\circ} 43' \text{ W}$). The shells were exposed in a gravel pit. The preservation state of the shells and the geology of the outcrops are described in Aitken (1987) and Aitken and Risk (1988). The C^{14} age of these outcrops is 8700 ± 330 yr BP (Waterloo dating no. 1200). The live modern specimens were collected from adjacent intertidal areas. Shell collections used in this study are archived in the Holocene section of the collections of the Department of Geology, McMaster University.

Thirty-five individuals each of sliced subfossil and modern *Mya truncata* shell pieces were prepared according to procedures described in Tevez et al. (1992) in order to obtain four matrix samples (modern and subfossil soluble; modern and subfossil insoluble). In addition, shell material was dialyzed in Spectrapor membrane tubing (m.w. cutoff: 12,000–14,000; cyl. dia.: 28.6 mm) against approximately 2 liters of a solution consisting of 200 g of EDTA di-sodium salt dissolved in distilled water. The resulting solution was adjusted to neutral pH and then dialyzed against 2.5 liters of distilled water for a period of one week. The contents of

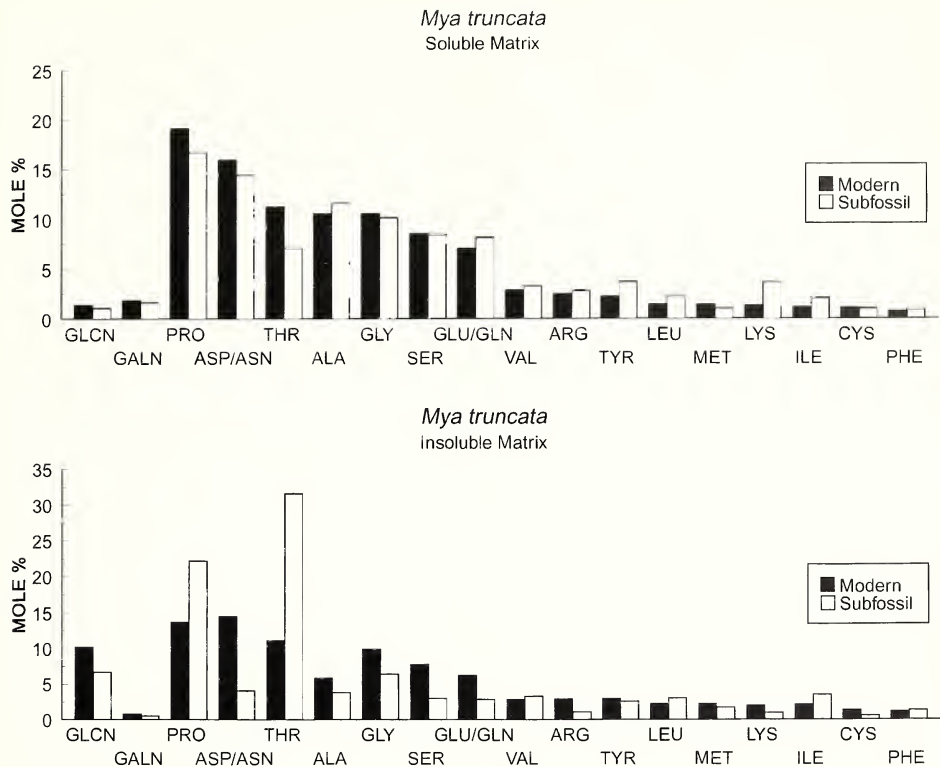


Figure 1. Composition of hydrolyzed matrix residues from *Mya truncata* shells.

the tubing were centrifuged in 50 ml centrifuge tubes. The insoluble matrix fraction appeared as a pellet at the bottom of the centrifuge tube. The supernatant containing the soluble fraction was collected by pipeting and introduced into fresh tubing and dialyzed against three changes of approximately 2.5 liters of distilled water. The contents of the tubing were then placed in flasks and dehydrated under conditions of high vacuum.

Preparation for and analysis by high-performance liquid chromatography (HPLC) of *M. truncata* matrix were done as follows: Matrix samples were dissolved in 2 ml of distilled water, mixed, and then 10 μ l of each sample were hydrolyzed in vacuo with gaseous 6N HCl at 105° C for 24 hr using a Picotag work station (Millipore Corporation, Waters Chromatography Division, Bedford, MA).

Hydrolysates were derivatized with phenylisothiocyanate (Cohen et al., 1984). The derivatized amino residues were separated by reverse phase HPLC using a 15 cm Picotag Amino Acid Column. Separation was achieved using a linear gradient shifting between polar eluent and nonpolar eluent in 14.5 min. at 42° C. Conditions for separation are described in Table 1. Elution was monitored by absorption at 254 nm. Identification and quantitation of the amino residues were performed by comparison of retention times and peak areas with those of simultaneously and identically processed external standards. The standards were from the following sources: amino acid standards (Pierce, 20088); amino sugar standards D-glucosamine hydrochloride (Sigma, G-4875) and D-galactosamine hydrochloride (Fluka, 48250).

Results

New data on the amino sugar and amino acid compositions of the soluble fraction of modern and subfossil *Mya*

Table 1. Gradient conditions for reverse phase HPLC

Time (min)	Flow Rate (ml/min)	*Eluent A (%)	**Eluent B (%)
0.0	1.0	100	0
11.5	1.0	54	46
11.7	1.0	0	100
12.2	1.0	0	100
12.5	1.5	0	100
13.0	1.5	100	0
20.0	1.5	100	0
20.5	1.0	100	0

*Eluent A (75 mM sodium acetate, 0.1% triethylamine, 5% acetonitrile, pH 5.75).

** Eluent B (60% acetonitrile in dH₂O).

truncata matrix, expressed as mean mole% of total amino residues detected, are presented in Table 2. The amount of soluble matrix recovered from the modern and subfossil shells was 706.35 pmol/ μ l and 2948.58 pmol/ μ l, respectively.

Data for the insoluble matrix from the same shells are presented by Risk et al. (in press) and are represented in histogram form in Figure 1, along with the data from the soluble matrix. These data were collected to complement a separate study of nuclear magnetic resonance analyses of protein/chitin ratios from *M. truncata* insoluble matrix.

Data were analyzed statistically for the two amino sugars and seventeen amino acids listed in Table 2. Values for soluble matrix compounds are given in Table 2 and Figure 1. Values for insoluble matrix compounds are tabularized in Risk et al. (in press) and also presented in Figure 1.

The modern and subfossil *Mya truncata* soluble/insoluble matrix samples each consisted of 35 randomly selected individual shells prepared in aggregate in order to provide sufficient material for HPLC analysis. Thus, amino sugar/amino acid compositions of each shell could not be determined. Analyses were conducted upon the following shell matrix fractions: modern soluble, subfossil soluble, modern insoluble, and subfossil insoluble. Three samples representing randomly drawn aliquots of the prepared matrix material were analyzed for the modern soluble, modern insoluble, and subfossil insoluble fractions; two samples were analyzed for the subfossil soluble fraction. Though statistical characterization of natural population variance within this experimental design was not possible, a statistical evaluation of analytical variation arising from the HPLC descriptions of these sets was accomplished. In addition, because the specimens were selected at random and involved a moderate number of individuals, it is expected that the findings are replicable at this level or in

any larger experimental design which would allow for broader population inferences.

The mole% data were converted by arcsine transformation prior to statistical analysis. This transformation is recommended for use on percentage data (Sokal and Rohlf, 1969). Two datasets, one combining modern and subfossil soluble matrix data, the other combining modern and subfossil insoluble matrix data, were analyzed by a one-way ANOVA procedure for the comparison of amino compound group means. After determining that each one-way ANOVA proved significant with an F probability $\leq .00005$ and with a two-tailed Levene test for homogeneity of variance probability $\leq .0005$, post hoc methods were employed to examine the pairwise comparisons between modern and subfossil group means on each of the 19 amino compound groups. Because multiple comparisons were made within this context, a multiple range test known as Student-Newman-Keuls with a significance level of .05 was selected. This test provided for a moderate control of Type I error rate (false differences) by conducting all pairwise comparisons between means using the studentized range distribution. These

Table 2. Amino sugar/amino acid compositions of modern and subfossil soluble matrices of *Mya truncata*, expressed as mean mole%. Numbers in parentheses are the reconverted arcsine transformed 95% confidence intervals (Sokal and Rohlf, 1969). n = 3 (modern); n = 2 (subfossil). * indicates amino sugar; remaining compounds are amino acids.

Compound	Modern	Subfossil
glen*	1.41 (0.66 - 2.39)	1.09 (1.05 - 1.14)
galn*	1.85 (1.46 - 2.28)	1.65 (1.53 - 1.77)
pro	19.1 (18.10 - 20.18)	16.7 (16.54 - 16.88)
asp/asn	15.9 (15.10 - 16.68)	14.4 (13.82 - 14.99)
thr	11.2 (10.70 - 11.73)	7.08 (7.06 - 7.10)
ala	10.5 (9.96 - 11.07)	11.6 (10.68 - 12.63)
gly	10.5 (10.18 - 10.79)	10.1 (10.05 - 10.11)
ser	8.52 (8.44 - 8.60)	8.43 (8.24 - 8.62)
glu/gln	7.01 (6.66 - 7.38)	8.14 (7.30 - 9.02)
val	2.85 (2.68 - 3.03)	3.26 (3.11 - 3.42)
arg	2.45 (2.05 - 2.88)	2.83 (1.99 - 3.82)
tyr	2.21 (2.01 - 2.43)	3.69 (3.44 - 3.94)
leu	1.43 (1.17 - 1.71)	2.30 (2.19 - 2.41)
met	1.40 (1.07 - 1.76)	1.05 (0.94 - 1.15)
lys	1.31 (0.01 - 4.36)	3.62 (3.19 - 4.06)
ile	1.14 (0.93 - 1.37)	2.09 (1.98 - 2.21)
cys	1.08 (1.04 - 1.12)	1.00 (0.42 - 1.82)
phe	0.71 (0.68 - 0.75)	0.91 (0.32 - 1.79)
his	trace	trace

pairwise comparisons were conducted in a stepwise fashion where means were ordered from highest to lowest and the greatest differences were the first tested (Sokal and Rohlf, 1969).

The comparisons made with the soluble matrix data furnished significant differences between the modern and subfossil groups for 8 of 19 amino compounds. These are ASP/ASN, GLU/GLN, ILE, LEU, LYS, PRO, THR, and TYR.

The comparisons made with the insoluble matrix data furnished significant differences between the modern and subfossil groups for 10 of 19 amino compounds. These are ALA, ARG, ASP/ASN, CYS, GLU/GLN, GLY, PRO, SER, THR, and GLCN.

Discussion

The means of several modern and subfossil amino acid data pairs are significantly different for soluble and insoluble matrix residues. In addition, the amino sugar glucosamine is significantly less abundant in subfossil insoluble matrix samples than in modern insoluble matrix samples. The fact that readily measurable, significant differences occurred within a discrete time interval suggests that differences in relative abundance of matrix monomers between modern and subfossil *Mya truncata* shells may be useful for geochronological purposes. Bada et al. (1978), for example, studied the diagenesis of the amino acids serine and threonine in foraminiferal tests and derived empirical equations that related amino acid ratios to time values. These equations were useful for estimating the age of sediment samples containing foraminiferans. For *M. truncata* insoluble matrix samples, Risk et al. (in press) suggested that changes in the protein/chitin ratio as determined by NMR or amino acid/glucosamine ratios as determined by HPLC may be geochronologically useful, because chitin degraded more rapidly than protein within a measured time interval. Our new findings indicate that glucosamine and galactosamine compositions of collected soluble matrix material from *M. truncata* shells are not a promising source of geochronological information for the investigated time interval because of the lack of significant change in subfossil values compared to modern values. Numerous amino acids (and/or amino acid ratios), however, offer possibilities for further investigation (e.g. ASP/ASN, GLU/GLN, ILE, LEU, LYS, PRO, THR, and TYR in the soluble matrix). Nevertheless, the apparent increase in the absolute amount of soluble matrix in subfossil compared to modern samples is surprising (one would expect a decrease as the matrix is broken down during diagenesis) and likely complicates defining the true composition of the subfossil soluble matrix.

Risk et al. (in press) reported a 3.25-fold decrease in the amount of insoluble matrix recovered from subfossil

shells compared to modern shells. The finding in this study of a 4.17-fold increase in the amount of soluble fraction residues in subfossil shells compared to modern shells therefore provides insights into the origin of the soluble residues obtained from *M. truncata*.

Both the insoluble and soluble matrices of invertebrates including mollusks are known to be affected by post-mortem hydrolysis of shell proteins (e.g. Goodfriend and Meyer, 1991; Goodfriend, 1992; Goodfriend et al., 1992) which result in racemization for particular monomers. For example, hydrolytic depolymerization may occur to the insoluble matrix, causing fragments to be solubilized. Hydrolysis of the soluble matrix is very rapid (<several hundred years) and lowers the molecular weight of soluble material. Considering the 8.7k BP age of the soluble matrix samples studied here, it is possible to envision at least two scenarios in which the composition of the collected soluble matrix may have been affected by post-mortem hydrolysis. First of all, hydrolysis of the original soluble matrix could have lowered the molecular weight of some of the soluble material below the 12-14 kDa level retained by the dialysis tubing used in sample collection, allowing this material to pass out of the tubing undetected. Secondly, hydrolysis of the insoluble matrix may have produced soluble material that was mobilized during the process of sample preparation and then retained by the dialysis tubing. Thus the "soluble matrix" recovered from the subfossil shells may differ in part from the soluble matrix of the modern shells as a result of the incorporation of a solubilized fraction from the insoluble matrix. The greater amount of soluble fraction recovered in the subfossil shells compared to the modern shells is evidence supporting this scenario. If this scenario is correct, then the "soluble matrix" collected for this study from the subfossil shells is an operational definition affected by diagenesis of other matrix components. It not only consists of original soluble matrix amino compounds but also likely contains solubilized fragments hydrolyzed from insoluble polymers.

We conclude that time-related changes in monomeric composition can be easily measured for both soluble and insoluble matrix residues of *Mya truncata*. We believe that these new findings should encourage further geochronological investigations of *M. truncata* organic matrix. Nevertheless, defining the true composition of the subfossil soluble matrix and inferring soluble matrix diagenesis is hampered because of contemporary degradation of the insoluble matrix.

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STENOSTEUS ANGUSTOPECTUS SP. NOV.
FROM THE CLEVELAND SHALE (FAMENNIAN) OF
NORTHERN OHIO WITH A REVIEW OF
SELENOSTEID (PLACODERMI) SYSTEMATICS

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ABSTRACT

A new species of *Stenosteus* Dean, *Stenosteus angustopectus*, is described from the Cleveland Shale (Famennian) of northern Ohio and is based on material recovered from the Interstate 71 Paleontological Salvage Project. *Stenosteus angustopectus* is characterized by: (1) long and narrow posterior ventrolateral plates, (2) a narrow median process on the anterior ventrolateral plate, (3) a tongue-in-groove joint between the anterior lateral and anterior dorsolateral plates, (4) a posterodorsal process on the suborbital plate, and (5) a posterior superognathal plate lamina that posteriorly is rotated 90°. This new species provides informative comparative material for a reevaluation of Dean's original descriptions of *Stenosteus glaber* and *Selenosteus brevis*, which were based on incomplete single specimens preserved in part and counterpart. *Stenosteus* and *Selenosteus* are retained as distinct genera. Uniting these two taxa are the denticulation pattern of the inferognathal and a relative reduction of the central plate length. *Stenosteus* and *Selenosteus* are united with *Gymnotracheilus* and *Melanosteus* based on the presence of a stem-like prehypophyseal region of the parasphenoid plate and a loose connection between the dermal cheek and head shield. Finally, Selenosteidae *sensu* Lelièvre, Feist, Goujet, and Blicek is retained (the relationships of *Bramosteus* remain unresolved).

Introduction

Several authors have evaluated the phylogenetic relationships among eubranchyothoracid arthrodires (cocosteo-morph and pachyosteo-morph arthrodires) including members of the subgroup Selenosteidae Dean, 1901 (e.g., see Miles and Dennis, 1979; Lelièvre et al., 1987; Gardiner and Miles, 1990, 1994; Carr, 1991, 1994). These evaluations have attempted to determine the relationships of North American, European, and Australian taxa; however, many of the North American forms lack a clear diagnosis or are based on fragmentary material thereby limiting the phylogenetic resolution within previous studies. Addressing this problem, Carr (1991, 1994) analyzed two North American taxa (*Heintzichthys gouldii* and *Gymnotracheus hydei*, respectively). This paper provides a further analysis of poorly known North American taxa.

Dean (1901) described two aspinothoracid arthrodires (*sensu* Miles and Dennis, 1979), *Selenosteus brevis* and *Stenosteus glaber*, from the Cleveland Shale of Ohio; each was based on a single specimen preserved in part and counterpart. Analyses of these taxa are problematic due to a lack of additional material and poor preservation. Dunkle and Bungart described several additional aspinothoracid arthrodires from the Cleveland Shale fauna (*Gymnotracheus*, 1939, see Carr, 1994, for a redescription; *Holdenius*, 1942; and *Paranylostoma*, 1945), but this material also is based on disarticulated and incomplete specimens. Inadequate material continues to limit systematic analyses of the Cleveland Shale fauna. In addition, the relationships between North American and other aspinothoracid arthrodires remain unclear. Fundamental to any systematic review are a phylogenetic diagnosis of *Selenosteus* and *Stenosteus* and the description of undescribed Cleveland Shale material. This paper describes a new species of *Stenosteus*, *Stenosteus angustopectus*, from the Cleveland Shale that provides the basis for a reevaluation of the holotypes for *Selenosteus brevis* and *Stenosteus glaber*. Finally, the new material augments Dean's (1901) original description and figures.

Anatomical abbreviations used in figures and listed at the end of the paper follow those of Dennis-Bryan (1987) and Carr (1991). Specimen number prefixes denote their respective institutions: CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; and AMNH, American Museum of Natural History, New York City. The suffix "id" when used to form taxonomic adjectives does not refer to the familial level in Linnean classification, but is used as a convenience for discussing informal taxonomic units.

Systematic Paleontology

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891

Family SELENOSTEIDAE Dean, 1901
(*sensu* Lelièvre et al., 1987)

Genus *STENOSTEUS* Dean, 1901
STENOSTEUS ANGUSTOPECTUS SP. NOV.

Figures 1–17

Name

L. angustus — narrow; *L. pectus* — breast, chest. Refers to the narrow ventral thoracic shield.

Diagnosis

Stenosteus angustopectus is a selenosteid arthrodire characterized by: (1) long and narrow posterior ventrolateral plates, (2) a narrow median process on the anterior ventrolateral plate, (3) a tongue-in-groove joint between the anterior lateral and anterior dorsolateral plates, (4) a posterodorsal process on the suborbital plate, and (5) a posterior supragenathal plate whose posterior lamina is rotated 90°.

Holotype

CMNH 8042 (Figures 1, 2, 5–8, 11, 13, 15, 16). The specimen possesses an incomplete head shield in external view with the pineal and rostral plates missing, a complete cheek assembly, anterior and posterior ventrolateral plates, an anterior dorsolateral plate, and fragmented posterior median ventral, median dorsal, possible posterior dorsolateral, and parasphenoid plates.

Additional Material

CMNH 8041: suborbital plates, inferognathal, sclerotics, posterior supragenathals, and perichondral ossifications. CMNH 8043 (Figures 9, 11, 13, 14, 15, 17): incomplete head shield, inferognathals, incomplete cheek with sclerotics, incomplete thoracic shield with anterior median ventral plate, and scapulocoracoid. CMNH 8044 (Figures 1, 3, 7, 12): incomplete head shield with isolated rostral, complete cheek assembly with sclerotics, lateral thoracic plates, perichondral ossifications, but lacking ventral plates and median dorsal plate. The left marginal and paranuchal plates are preserved in internal view. CMNH 8045 (Figures 1, 2, 7): complete head shield in external view, inferognathals, fragmented and incomplete thoracic shield, incomplete cheek with sclerotics, and perichondral ossifications. CMNH 8046 (Figures 4, 10): incomplete head shield in internal view with an isolated rostral plate (lacking gnathal plates and parasphenoid), cheek with sclerotics, and incomplete thoracic shield. CMNH 9598: anterior ventrolateral plates, impression of the posterior suborbital plate, and fragmented posterior median ventral plate and scapulocoracoid. CMNH 9931: posterior ventrolateral plate.

Table 1 documents the presence of diagnostic characters used to relate the referred material to *Stenosteus angustopectus*. Several equivocal characters (equivocal at a level capable of resolving the relationships of *Selenosteus*

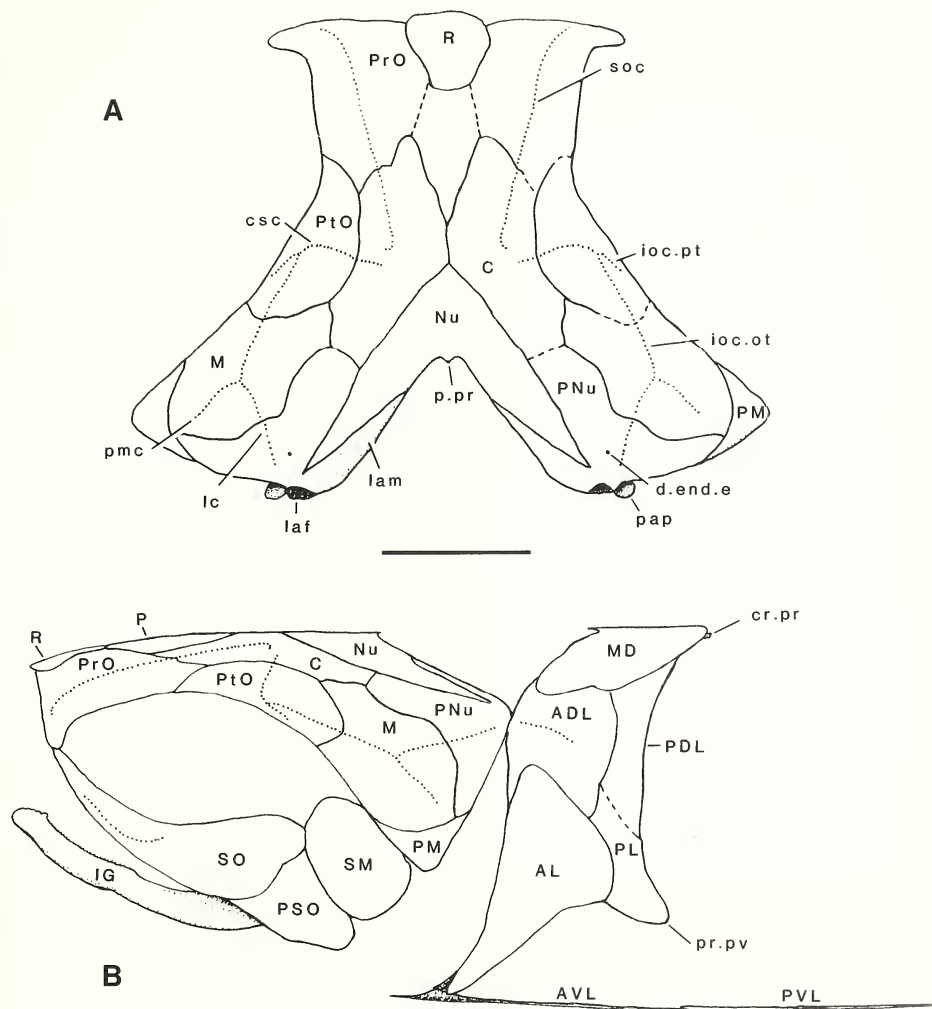


Figure 1. *Stenosteus angustopectus* sp. nov. A, a reconstruction of the head shield in dorsal view. Based on a composite of photographic tracings from CMNH 8042, CMNH 8044, and CMNH 8045. The reconstruction portrays the secondary flattening seen in all the specimens. B, a reconstruction of the head and thoracic shields in left lateral view. Scale bar = 5 cm.

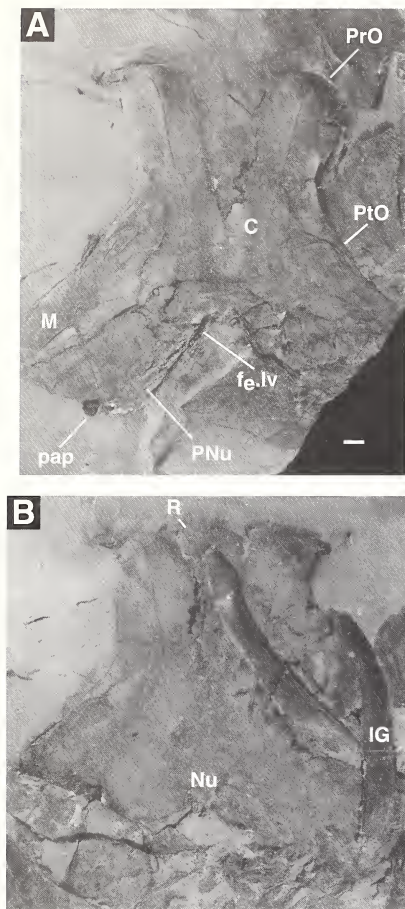


Figure 2. *Stenosteus angustopectus* sp. nov. A, head shield of holotype (CMNH 8042) in dorsal view and B, head shield of CMNH 8045 in dorsal view. Scale bar = 1 cm.

and *Stenosteus* to other selenosteids) are included to distinguish *Stenosteus* specimens from *Selenosteus*. There are no contradictory features between the referred material and *Stenosteus angustopectus*.

Occurrence

The holotype and referred material was collected by field crews from the Cleveland Museum of Natural History dur-

ing the Interstate 71 Paleontological Salvage Project (1966–1967). Specimens were recovered from the Cleveland Shale at the intersection of West 130th Street and Interstate 71, Cleveland, Ohio.

Stratigraphy

The Cleveland Shale is in the Famennian Stage of the Devonian System. The *Stenosteus angustopectus* material was taken from the *Heintzichthys gouldii* zone formerly exposed in a quarry located at West 130th Street and Interstate 71, which is now filled in and covered by the interstate (Carr, 1991, based on a personal communication from William Hlavin; however, the detailed stratigraphic position for this unit within the Cleveland Shale is unclear). The Cleveland Shale, in the Cleveland area, overlies the Chagrin Shale and is itself overlain by the Bedford Shale.

Description

Head Shield

General features. The head shield (Figures 1–7) is composed of 15 individual plates; three unpaired median plates (rostral, pineal, and nuchal) and six paired plates (preorbital, postorbital, central, marginal, paranuchal, and postmarginal). There is no evidence for the presence of postnasal plates and they are assumed to be lost phylogenetically. All plates are secondarily deformed, that is, flattened during diagenesis. The contact surfaces between adjacent plates are denoted as either a contact face on the visceral surface or an overlap area on the external surface (after Dennis and Miles, 1979a).

Rostral (R). The rostral and pineal plates, as a rule, are sutured weakly to adjacent plates resulting in either their displacement or loss during fossilization with the one exception of CMNH 8045 (missing in the holotype, CMNH 8042). The rostral plate (Figures 1, 2B, 3A) is triangular in shape possessing a broad anterior margin with a shallow descending face. In CMNH 8045 (Figure 2B), the descending face possesses a roughened texture. Overlap patterns are not completely discernible, although a preorbital contact face appears to be present on the internal surface of CMNH 8044 (cf. PrO, Figure 3A). A ventral anterior thickening (a.th, Carr, 1991, fig. 4A) is absent.

Pineal (P). The pineal plate (found in CMNH 8045 only; Figures 1, 2B) separates the preorbital plates and the anterior or third of the central plates. The nature of the preorbital-pineal overlap is unclear based on available material. An absence of an apparent pineal contact face on the visceral surface of the rostral plate suggests that the pineal plate overlies the rostral. An external pineal opening is absent (the opening seen in CMNH 8045, Figure 2B, is not centrally located and represents damage to the bone).

Nuchal (Nu). The nuchal plate (Figures 1, 2A, B) is triangular in external view with a deep posterior embayment that in life would have left the posterior neurocranium and

Figure 3. *Stenosteus angustopectus* sp. nov. (CMNH 8044). A, rostral plate in internal view and B, left postmarginal plate in external view. Scale bars = 1 cm.

presumed synarcual articulation exposed, i.e., uncovered by dermal bone. The sides of the embayment form an angle of *ca.* 80° in the holotype (CMNH 8042; CMNH 8045 = *ca.* 100°). A median nuchal process is present (p. pr., Figure 1). The nuchal extends anteriorly between the central plates to the level of their centers of ossification. Posterolateral nuchal alae extend to nearly the posterior margin of the head shield. A shallow shelf lateral to the median process and facing dorsally may represent the site of attachment for the levator muscles of the head (*f.c.lv*, Figure 2A). The nuchal is not preserved in internal view.

Preorbital (PrO). The preorbital plate (Figures 1, 2A, B) possesses a strongly developed preorbital dermal process. The anterolateral corners of the head shield are downturned (Figure 2) with the body of the rostral plate apparently not participating in a descending face. This downturned condition of the preorbital plate may reflect the compression of the head shield anterior to the internal thickenings of the preorbital dermal process (in *Gymnotracheus* and *Heintzichthys* the preor-

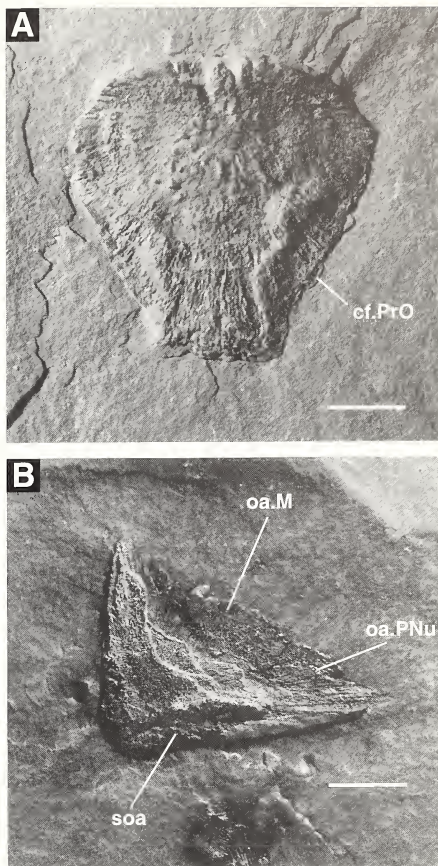


Table 1. A table of diagnostic characters used to relate the referred material to *Stenosteus angustopectus* sp. nov. A superscript (1) indicates autapomorphic features of *S. angustopectus* based on the holotype, CMNH 8042. A superscript (2) indicates secondary autapomorphic features (missing in the type) that are found in referred specimens with a clear link to the type. Remaining characters represent equivocal features at a higher level of analysis, but provide evidence to distinguish *Stenosteus* specimens from *Selenosteus*. There are no contradictory features between the referred material and *Stenosteus angustopectus* sp. nov. An (X) indicates that the character is preserved in the respective specimen with an empty cell indicating its absence.

Diagnostic Character	8042 (holotype)	8041	8043	8044	8045	8046	9598
PVL ¹	X		X				
AVL process ¹	X					X	X
ADL-AL suture ¹	X		X (AL only)			X	
SO process ¹	X	X	X	X		fragmented	
PSG ¹	X	X					
PL process ²			X	X			
C-M contact	X		X	X	X		
MD shape	fragmented				X	X	

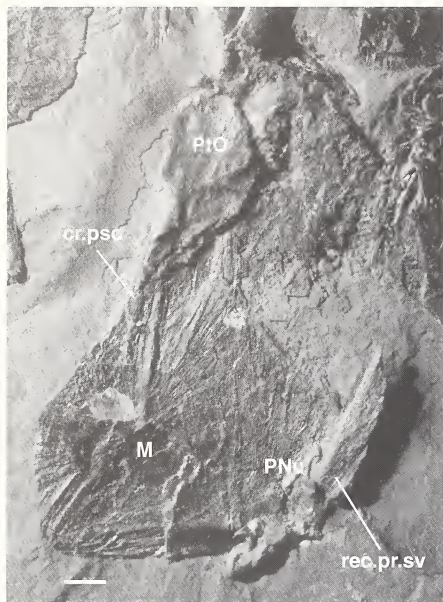


Figure 4. *Stenosteus angustopectus* sp. nov. (CMNH 8046). Right postorbital, marginal, and paranuchal plates in internal view. Scale bar = 1 cm.

bital plate is expanded anteriorly over the rhinocapsular region, Carr, 1994, p. 7, fig. 3). The supraorbital sensory line groove (soc, Figure 1) traverses the preorbital plate terminating medial to the dermal process. The ratio of parasagittal lengths between the preorbital and central plates is *ca.* 0.88 in the holotype (Pro/C, CMNH 8042; CMNH 8045 = *ca.* 0.80) and to the postorbital plate is *ca.* 1.1 (Pro/PtO, CMNH 8042; CMNH 8045 = *ca.* 1.1). The postorbital plate, which lies at an angle to the sagittal plane, is subequal to the preorbital plate when measured along its greatest dimension (Pro/PtO = *ca.* 0.92 and *ca.* 1.04 in CMNH 8045 and 8042 respectively). Internal views are not available.

Postorbital (PtO). The postorbital plate (Figures 1, 2A, B, 4) is narrow (length/width in CMNH 8042 = *ca.* 2.6 and CMNH 8045 = *ca.* 2.7) with a postorbital process absent. There is a subtle convexity along the lateral border of this plate. The grooves for the postorbital (ioc.pt, Figure 1) and otic (ioc.ot, Figure 1) branches of the infraorbital sensory line form a closed angle (less than 45°). A central sensory line groove is present (csc, Figure 1) and terminates before the medial edge of the plate. In CMNH 8045 the central sensory line groove is continuous with its extension onto the central plate.

Internally, CMNH 8046 (Figure 4) possesses a continuation of the supraorbital vault, which is bounded medially by a low ridge. This ridge continues posterolaterally as the posterior supraorbital crista (cr.pso, Figure 4) to the lateral margin of the head and may continue for a very short distance onto the marginal plate. Suture lines between the preorbital and marginal plates are unclear in the one internally exposed specimen (CMNH 8046). If the supraorbital crista does continue onto the marginal plate it is limited to the most antero-lateral portion of the plate. Finally, the inframarginal crista extends forward to connect with the supraorbital vault.

Central (C). The central plates (Figures 1, 2A, B) are separated anteriorly by the pineal plate and posteriorly by the nuchal plate reducing the central-central contact to approximately one sixth of their total longitudinal length. Two sensory line grooves are present. A continuation of the groove for the supraorbital sensory line (soc, Figure 1) is present and terminates near the ossification center in a J-shape that opens laterally. A continuation of the central sensory line groove (csc, Figure 1) from the postorbital plate is present bilaterally in CMNH 8042, 8043, and 8045, although distinct and continuous with the central sensory line groove on the postorbital plate only in CMNH 8045. Overlaps are difficult to discern, although the postorbital plates are typically displaced on top of the central plates suggesting the latter are overlapped by the postorbital plates. It appears that the central plates overlap the nuchal plate and preorbital plates (in part). A central-marginal plate contact is present, which is approximately equal to the central plate's length of contact with the paranuchal plate. In CMNH 8045 (Figure 2B), the central and postorbital plates extend anteriorly to a similar level; whereas, in CMNH 8042 (Figure 2A) the central plates project further anteriorly along the medial edge of the preorbital plate. Internal features are not distinguishable on the internally exposed material.

Marginal (M). The marginal plate (Figures 1, 2A, B) is present in the orbital margin (refer to the discussion of Character 3 below) and is in contact with the central plate. Carr (1991) noted that aspinotoxaracid arthrodires typically lack this contact (e.g., *Heintzichthys*, *Gorgonichthys*, and *Pachyosteus*) with *Rhinosteus* possessing a contact and *Selenosteus* being polymorphic. The Cleveland Museum of Natural History "Selenosteus" material used in the 1991 analysis is assigned here to *Stenosteus*. Continuing onto the marginal plate, the postotic branch of the infraorbital sensory line groove extends to the ossification center. Here, the groove continues as the main lateral line (lc, Figure 1) onto the paranuchal plate. A postmarginal sensory line groove (pmc, Figure 1) extends posterolaterally from the ossification center and terminates before reaching the plate margin. The angle formed by the postmarginal and main sensory line grooves is *ca.* 85–90°. Equidimensional angles are formed by the latter two grooves and the postotic infraorbital line groove (130–135°).

Internally (Figure 4), the inframarginal crista extends

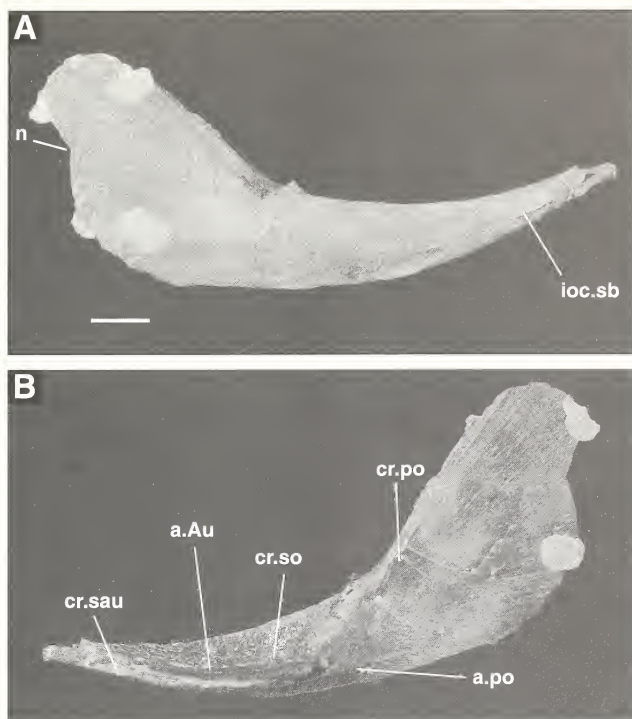


Figure 5. *Stenosteus angustopectus* sp. nov. Right suborbital plate (CMNH 8042) in A, external and B, internal views. Scale bar = 1 cm.

from the margin of the supraorbital vault to the marginal plate ossification center. From there, it extends beneath the postmarginal sensory line decreasing in height to the plate's edge. A second thickening extends from the ossification center beneath the main lateral line. As noted above, the supraorbital crista may extend onto the marginal plate. This extension does not necessarily indicate the involvement of the marginal plate in the orbital border (see discussion of Character 3 below).

Postmarginal (PM). The postmarginal plate (Figure 1; present in CMNH 8044, 8045, and 8046; missing in the holotype, CMNH 8042) is triangular in shape with the anteroventral and posterior margins forming an angle of ca. 72–80° (Figure 3B). The plate is overlapped by the paranuchal (oa.PNu, Figure 3B) and marginal (oa.M, Figure 3B) plates with the latter forming the larger overlap. A

groove for the postmarginal sensory line is absent. The posterior margin is depressed forming a suborbital area (soa, Figure 3B; Dennis-Bryan, 1987, fig. 5), which appears to be limited to the postmarginal plate. Internally (CMNH 8045), a continuation of the inframarginal crista is absent.

Paranuchal (PNu). The main lateral line groove traverses the paranuchal plate (Figures 1, 4). Medial to the groove, an external endolymphatic pore (d.end.e, Figure 1) is present. A narrow process projects laterally to overlap the postmarginal plate. The posterior plate margin is transverse or slightly convex (in contrast to *Selenosteus brevis* where the margin is embayed). A very small postnuchal process (Carr, 1991, character 30) extends to the tip of the nuchal ala. The postnuchal process is continued as a well-developed shelf on the descending posterior face of the head shield (lam, Figure 1; a similar shelf is seen in *Gymnotrachelus*, Carr, 1994, fig. 5). It is possible that this shelf represents an expansion of the attachment site for the levator muscles of the head. A par-articular process (pap, Figures 1, 2A) is strongly developed.

Internally (Figure 4), the nuchal thickening is continued laterally along the posteromedial border of the paranuchal

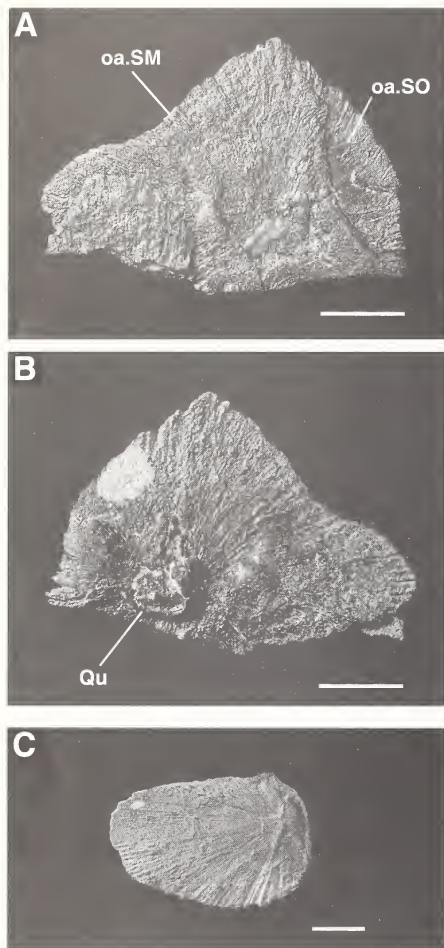


Figure 6. *Steuosteus angustopectus* sp. nov. (CMNH 8042). Right postsuborbital plate in A, external and B, internal views. C, right submarginal plate in internal view. Scale bars = 1 cm.

plate. An additional thickening continues from the articular fossa under the posterolateral ala of the paranuchal plate (along the posterior border toward the postmarginal plate). A distinct depression for the cucullaris muscle is not discernible. Along the paranuchal portion of the transverse occipital arch, a recess for the supravagal process of the

neurocranium may be present (rec.pr.sv, Figure 4). It appears as a shallow step since the ventral cover for the recess has been lost.

Cheek Plates

General features. The three paired plates of the cheek (suborbital, posterior suborbital, and submarginal; Figures 5, 6A, B and 6C, respectively) do not fuse to the head shield (a primitive feature of aspinothoracid arthrodires). The ovoid to subrectangular submarginal plate loosely abuts a very small overlap area on the postsuborbital. Its shape is in contrast to the elongate submarginal of basal aspinothoracid arthrodires. The cheek plates are secondarily deformed, that is, flattened during diagenesis.

Suborbital (SO). The shape of the suborbital plate (Figures 1B, 5) is similar to that of other selenosteids with an expanded posterior region ("blade") that tapers gradually to form an anterior suborbital region ("handle"). A notch is seen along the posterior margin (n, Figure 5A) delimiting a posterodorsal process. The suborbital branch of the infraorbital sensory line groove (ioc.sb, Figure 5A) is present; however, it is limited to the "handle" region. The groove parallels the internal autopalatine depression and separates the outer surface into asymmetrical regions with the ventral one being smaller (in contrast to *Gymnotrachelus*, where the ventral region is larger, Carr, 1994). A supraoral sensory line groove is absent.

Internally, subocular (cr.so, Figure 5B), subautopalatine (cr.sau, Figure 5B), and postautopalatine (a.po, Figure 5B; = R3 of Heintz, 1932) cristae and an autopalatine depression (a.Au, Figure 5B) are present on the surface of the "handle" portion. The subautopalatine crista is broken; however, there is no evidence for the presence of a contact face for the posterior superognathal as seen in *Dunkleosteus* and *Eastmanosteus* (Carr, 1991, cf. PSG, fig. 5B; Dennis-Bryan, 1987, figs. 9, 13). A low postocular crista (cr.po, Figure 5B) is present. The postautopalatine posteroventral thickening (a.po, Figure 5B; = R3 of Heintz, 1932) extends a very short distance from the confluence of the other three cristae.

Postsuborbital (PSO). The postsuborbital plate (PSO, Figures 1B, 6A, B) is roughly triangular in outline. Anteriorly there is an overlap area for the suborbital plate (oa.SO, Figure 6A) and posteriorly there is a small and nearly indistinct overlap area for the submarginal plate (oa.SM, Figure 6A). Dorsally, both of these overlap areas approach the plate's apex resulting in little or no separation between the submarginal and suborbital plates (a distinct gap between the suborbital and submarginal plates is present in *Gymnotrachelus*). The postsuborbital plate forms a small notch along the posterior border of the suborbital plate.

Internally, CMNH 8042 possesses a perichondrally ossified quadrate (Qu, Figure 6B) with the condylar region located near the ventral plate margin. The presence of a detent process cannot be determined (Gardiner and Miles, 1990,

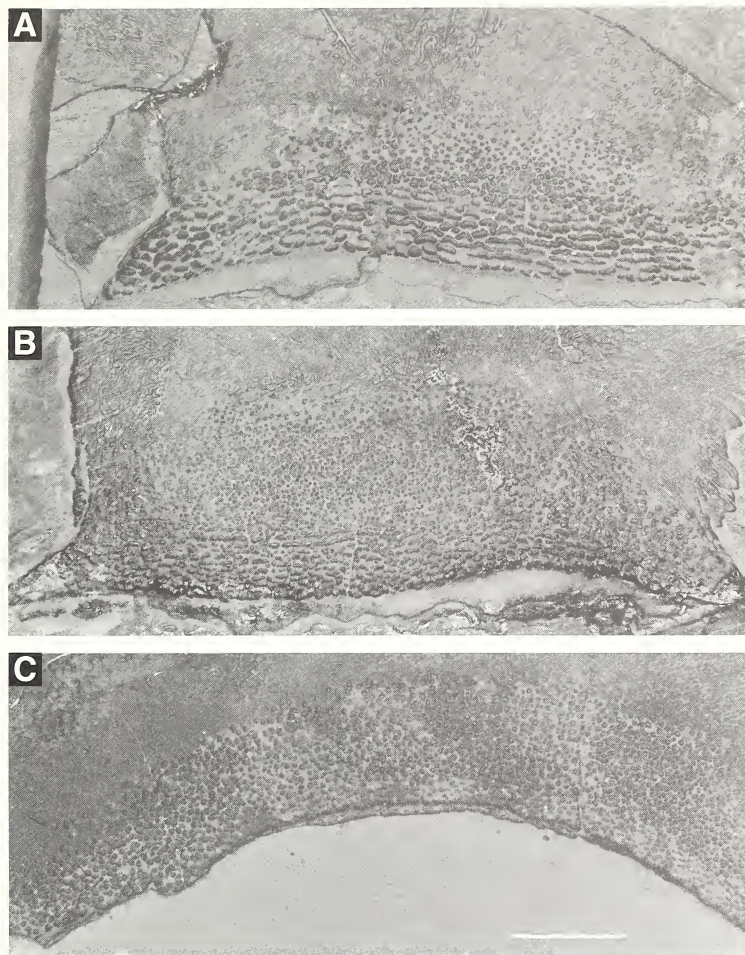


Figure 7. *Stenosteus angustopectus* sp. nov. A, sclerotic plate from holotype (CMNH 8042) showing rod-like medial denticles. B, sclerotic plate from CMNH 8044 showing intermediate condition. C, sclerotic plate from CMNH 8045 showing punctate pattern of denticles. Scale bar = 0.5 cm.

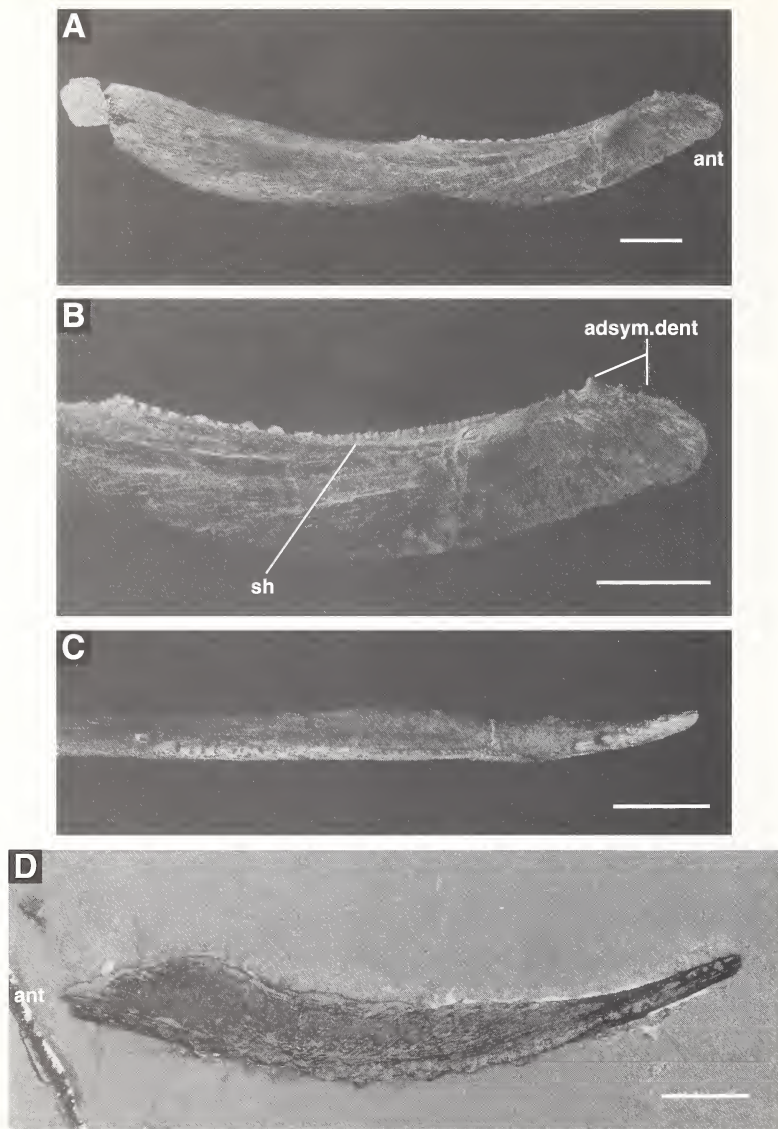


Figure 8. *Stenosteus angustopectus* sp. nov. (CMNH 8042). A, right inferognathal in lateral view and B, a close-up of the occlusal region. C, dorsal view of the occlusal region of the right inferognathal. D, right posterior superognathal in ventral view. A–C, scale bars = 1 cm. D, scale bar = 0.5 cm.

pr.det; see also Dennis and Miles, 1979b, fig. 10). This feature, when present, can be recognized on the dorsal extending ridge of the quadrate as a "stout, forward pointing process situated above the posterior end of the condylar area" (Stensiö, 1963, p. 236). Dennis and Miles (1979a, fig. 16) also interpreted an unossified area on the quadrate in *Cammiopiscis concinnus* as evidence for the presence of a cartilaginous detent process. Gardiner and Miles (1990, p. 196) consider the detent process to be an eubranchyothoracid synapomorphy, but missing (secondarily lost) in *Brachyosteus*, brachydeirids, trematosteids, and leiosteids. Among aspinothoracid arthrodires a detent process is known to be present in *Heintzichthys* (Carr, 1991, fig. 6B). The large number of taxa for which this feature is unknown makes it difficult to critically analyze, although, its known distribution is consistent with the interpretation of Gardiner and Miles (1990).

Submarginal (SM). The submarginal plate (Figures 1B, 6C, 12) is rectangular to oval in shape with the longest dimension paralleling the head shield margin. The plate is narrower anteriorly with the ossification center located posteriorly. An internal groove for the hyomandibula is absent.

The reconstructed position of the submarginal plate based on known plate overlaps (Figure 1B) suggests a possible anterior shift relative to the condition seen in *Gymnotracheus* (Carr, 1994, fig. 2B). This shift has resulted in the distancing of the suborbital plate from the head shield margin forming a large gap between the head shield and cheek plates.

Sclerotic (scler). Four ornamented sclerotic plates are associated with each eye. The ornament consists of punctate tubercles peripherally that coalesce centrally to form short rod-like tubercles which parallel the plate's central margin. The pattern of coalescence is clearly seen in the holotype (CMNH 8042; Figure 7A) and less so in CMNH 8044 (Figure 7B). CMNH 8045 (Figure 7C) and 8046 lack a coalescing pattern with only punctate tubercles present. The degree of coalescence is not correlated with size (based on a comparison of inferognathal size with the pattern of sclerotic plate ornament).

Gnathal Plates and Parasphenoid

General features. Two paired gnathal elements are present (inferognathal and posterior superognathal plates; Figures 8A–C, and 8D respectively). Anterior superognathal plates are not represented on any of the Cleveland Museum specimens. Fragmented parasphenoids are present in the holotype (CMNH 8042) and CMNH 8043. The parasphenoid does not appear to articulate with the anterior superognathals based on the anterior surface of the parasphenoid.

Inferognathal (IG). The occlusal surface forms approximately one half the total length of the inferognathal (Figures 8A–C). A single row of denticles is found along the occlusal surface in the holotype (CMNH 8042) with other specimens showing increasing wear with age. A narrow shelf (sh,

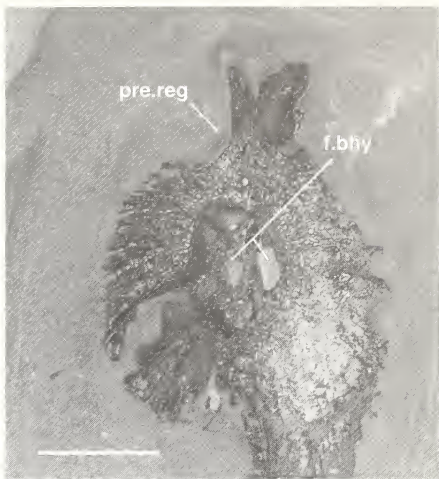


Figure 9. *Stenosteus angustopectus* sp. nov. Parasphenoid plate (CMNH 8043) in ventral view. Scale bar = 0.5 cm.

Figure 8B) is present lateral to the row of denticles. Adsymphyseal denticles (adsym.dent, Figure 8B) are present with the largest typically located at the apex of the adsymphyseal region (type specimen with five or possibly six adsymphyseal denticles on the left inferognathal and four on the right with the most anterior ones missing possibly due to wear). An additional large denticle is present on the occlusal side of the apex. The transition from large denticles to the fine denticles forming the remaining occlusal region is located above the center of ossification. The large denticle forming the apex is assumed to be homologous with the anterior cusp of dunkleosteids. The number of denticles per centimeter varies along the occlusal region with a larger number anteriorly (denticles per centimeter in the holotype, CMNH 8042: 18 per centimeter anteriorly and 10 per centimeter posteriorly).

Posterior superognathal (PSG). The posterior superognathal plate (Figure 8D) is similar in shape to those in *Rhinosteus* (Stensiö, 1963, Pl. 20, figs. 2–3) and *Gymnotracheus* (Carr, 1994, fig. 9). The posterior superognathals are elongate with a single lateral row of denticles. The denticles are typically worn (denticles per centimeter in the holotype, measured posteriorly only, 12 per centimeter). A distinct medial process is absent. Anteriorly, a medial shelf is developed which gently tapers until it is lost just before the posterior border. In *Gymnotracheus*, a distinct step is seen separating anterior and posterior regions; however, this feature is absent in *Stenosteus angustopectus*. In



Figure 10. *Stenosteus angustopectus* sp. nov. Median dorsal plate (CMNH 8046) in external view. Scale bar = 1 cm.

further contrast with *Gymnotrachelus*, the originally horizontal posterior shelf is rotated 90° forming a vertical wall with denticles along its ventral border. *Selenosteus brevis* possesses accessory denticles on the posterior portion of the posterior superognathal plate.

The posterior superognathal of *Melanosteus* differs from that in *Stenosteus angustopectus* and *Gymnotrachelus* in being a much deeper structure with a thickening or concentration of denticles located at the apex of the ventral angle (Lelièvre et al., 1987, Pl. 3 [figs. D, E]). Additional denticles are visible along the ventrolateral margin. In contrast, the dorsoventrally flattened posterior superognathals in *Stenosteus angustopectus* and *Gymnotrachelus* possess a series of denticles evenly distributed along their lateral margins (Figure 8D; Carr, 1994, fig. 9A; it is interesting to note that if figs. D and E [Pl. 3] in Lelièvre et al., 1987, are reinterpreted as dorsal and ventral views respectively, then the posterior superognathals of *Melanosteus* and *Stenosteus angustopectus* would share similar outlines with laterally placed denticles; however, the interpretations of these structures have been reconfirmed by Lelièvre, personal communication).

Parasphenoid (Psp). The parasphenoid is poorly preserved and present in only two specimens (the holotype, CMNH 8042, and CMNH 8043). CMNH 8043 (Figure 9) shows a parasphenoid in ventral view. Paired buccohy-

pophysal foramina (f.bhy, Figure 9) are situated near the center of the plate, although it is not clear that anterior and posterior extensions of the plate are fully represented. A ventral groove is absent. The plate is broadest at the level of the foramina with the prehypophysial region rapidly narrowing to form a stemlike anterior projection. A stemlike prehypophysial region (pre.reg, Figure 9) is reminiscent of the condition seen in *Melanosteus* (Lelièvre et al., 1987, Pl. 2 [figs. C–E]) and *Gymnotrachelus* (Carr, 1994, fig. 9B). A second specimen (the holotype, CMNH 8042) may represent a fragmented parasphenoid in dorsal view. A deep buccohypophysial depression is present with the lateral walls of the depression deeply notched. Anterior and posterior extensions of this second parasphenoid are not preserved.

Dermal Shoulder Girdle

General features. The dermal thoracic shield is clearly composed of 15 individual plates (Figures 10–16); three unpaired median plates (median dorsal, anterior median ventral, and posterior median ventral) and six or possibly seven paired plates (anterior dorsolateral, posterior dorsolateral, anterior lateral, posterior lateral, anterior ventrolateral, and posterior ventrolateral, with a possible presence of interlateral plates). The spinal plates are not present in any of the *Stenosteus* material and are assumed to have been lost phylogenetically. Interlateral plates are not recognized in any of the specimens. It is not clear how the lateral and ventral portions of the thoracic shield are interconnected and whether the interlateral plates are either phylogenetically

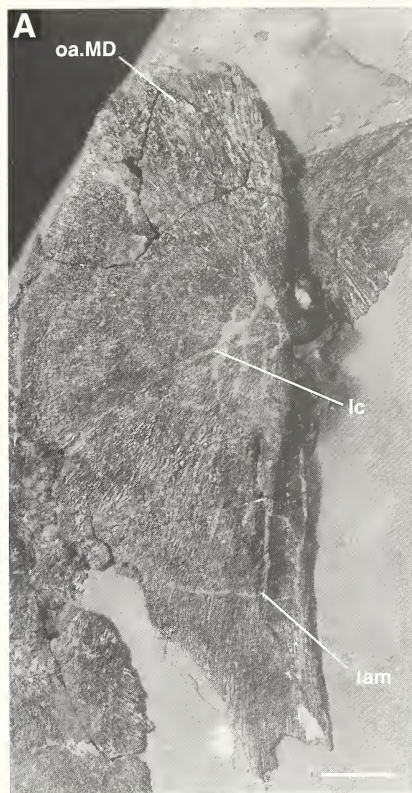


Figure 11. *Stenosteus angustopectus* sp. nov. Right anterior or dorsolateral plate in A, external (CMNH 8042) and B, internal (CMNH 8043) views. Scale bars = 1 cm.

lost or just missing from available material (in *Gymnotrachelus*, only a single putative interlateral plate is preserved which is reduced to a simple elongated plate, Carr, 1994, fig. 11). It should be noted that some aspinothoracid arthrodires, specifically the trematosteids *Parabelosteus* and *Brachyosteus* have lost the interlateral plate (Lelièvre, personal communication; Denison, 1978). The phylogenetic distribution of this feature (loss of the interlateral plates) remains unclear. All plates are secondarily deformed, that is, flattened during diagenesis.

Median dorsal (MD). The median dorsal plate (Figures 1B, 10) of the holotype (CMNH 8042) is incomplete, but shows that the anterior margin is deeply embayed. CMNH 8045 and 8046 (Figure 10) possess a narrow anterior medial process. This process is not supported by an internal keel. The anterolateral margins are slightly notched in the region of the anterior dorsolateral plate and posterior

dorsolateral plate contact. The posterior margin is gently embayed in CMNH 8046 and more strongly embayed in CMNH 8045 (a shallow embayment is suggested in the holotype). A non-spatulate carinal process (cr.pr, Figure 10) is visible beyond the posterior edge of the plate in CMNH 8045 and 8046. The internal surface is not exposed in available material.

Anterior dorsolateral (ADL). The anterior dorsolateral plates (Figures 1B, 11) are subrectangular in outline with a deeply embayed ventral margin (height/width = ca. 2.8). The anterior dorsolateral plate is overlapped by the median dorsal plate (oa.MD, Figure 11A) with a short process extending anterior to the median dorsal plate and forming part of the nuchal gap border. Ventrally, there is an overlap area for the anterior lateral plate (oa.AL, Figure 11). Anteriorly, the anterolateral overlap area possesses a posteriorly directed lamina (lam, Figure 11A) forming a

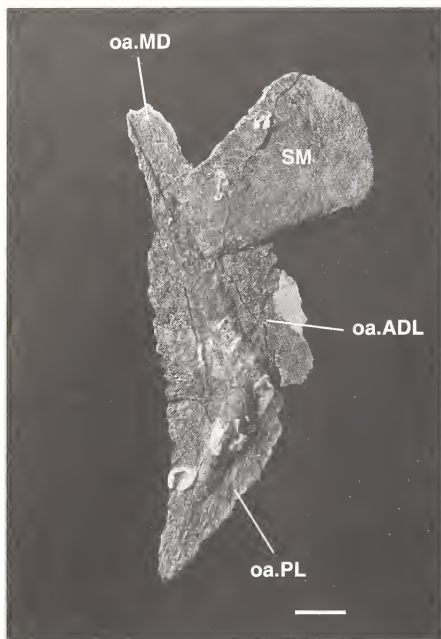


Figure 12. *Stenosteus angustopectus* sp. nov. Right posterior dorsolateral plate (CMNH 8044) in external view. Scale bar = 1 cm.

groove beneath. Apparently, a medial lamina on the anterolateral plate forms a tongue-in-groove junction with the anterior dorsolateral plate. The anterodorsal surface of the flange forms part of the postbranchial embayment.

A continuation of a groove for the main sensory line (lc, Figure 11A) extends to about midplate. The groove is directed posteroventrally (Figure 11A), although its ventral projection is less than that seen in the ventral groove of the main lateral line in coccosteomorph arthrodires (lc.v1 of Miles, 1971, fig. 108). Both a glenoid condyle (kd, Figure 11B) and subglenoid process (pr.sg, Figure 11B) are well developed and form part of a strong articulation between the head and thoracic shields.

Posterior dorsolateral (PDL). The posterior dorsolateral plate (Figures 1B, 12) is crescent shaped with a serrate posterior margin (CMNH 8042, length/width = ca. 3.1 with the length measured along the greatest dimension and the width perpendicular to length). The external plate face shows three overlap areas: a median dorsal plate

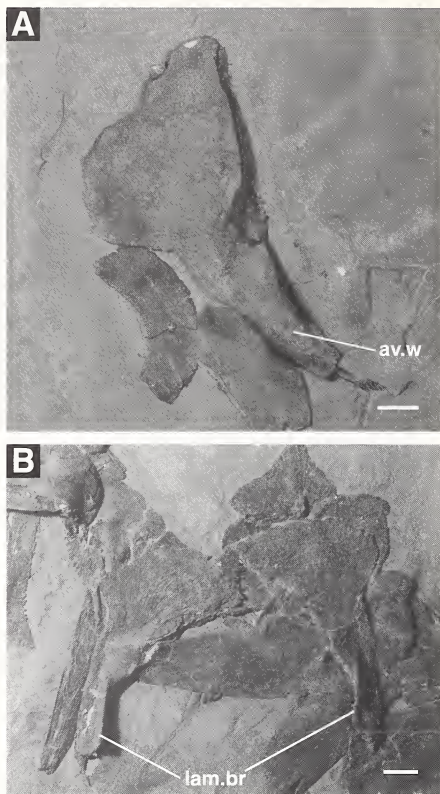


Figure 13. *Stenosteus angustopectus* sp. nov. A, right anterior lateral plate (CMNH 8042) in external view. B, right and left anterior lateral plates (CMNH 8043) in internal view. Scale bars = 1 cm.

overlap (oa.MD, Figure 12), an anterior dorsolateral plate overlap (oa.ADL, Figure 12), and a posterior lateral plate overlap (oa.PL, Figure 12). There is no extension of a lateral line groove onto the plate. Only a dorsal fragment of the posterior dorsolateral plate is exposed on the holotype (CMNH 8042).

Anterior lateral (AL). The anterior lateral plate (Figures 1B, 13) is triangular in outline with the external anteroventral wing (av.w, Figure 13A) tapering to its ventral end. The broader dorsal region and ventral region form an angle of ca. 145° along the anterior margin (ca.

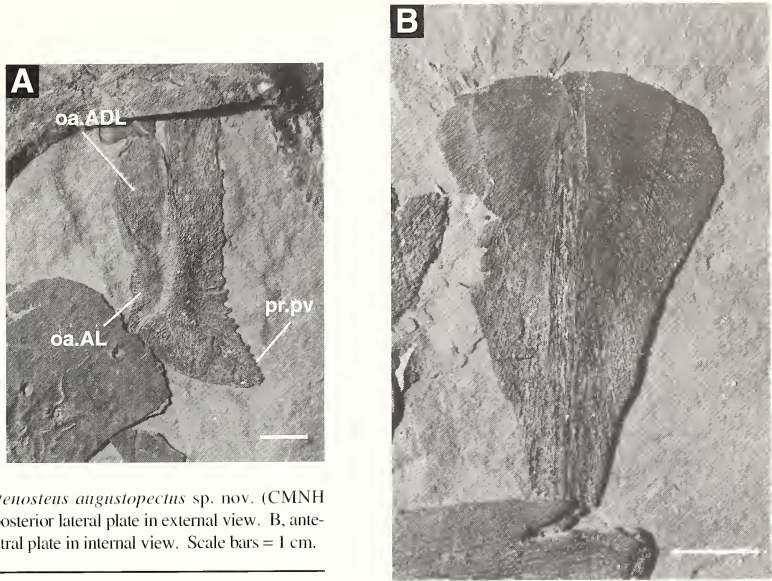


Figure 14. *Stenosteus angustopectus* sp. nov. (CMNH 8043). A, left posterior lateral plate in external view. B, anterior median ventral plate in internal view. Scale bars = 1 cm.

135° in CMNH 8044 and in CMNH 8043 *ca.* 140° on the right and *ca.* 156° on the left, although these latter two estimates are based on internal views). Dorsally, the anterior margin consists of two laminae. The medial lamina forms a tongue-in-groove joint with the anterior dorsolateral plate. The external lamina does not appear to extend beyond the anterior edge of the anterior dorsolateral plate, thus, the anterior lateral plate lacks a distinct obstantic process overlying the postbranchial embayment, which houses the posterolateral margin of the head shield.

Internally, a well-developed branchial lamina is present (lam.br, Figure 13B).

Posterior lateral (PL). The posterior lateral plate (Figures 1B, 14A) is not exposed on the holotype (CMNH 8042), but is rhomboidal in outline with the posteroventral corner forming a short process (pr.pv, Figure 14A). This process is directed posteroventrally forming part of the pectoral fenestra border. A similar situation is seen in *Heintzichthys gouldii* (Carr, 1991, figs. 2, 10B); although, the process is much more elongate in *Heintzichthys*.

Table 2. A data matrix for the taxa and characters used in the current analysis (11 taxa, 18 characters, (?) = missing data, (–) = cases where the character is not applicable).

Trematosteidae	1 1 0 1 0	0 0 0 0 0	0 0 0 0 0	1 2 ?
Brachydeiridae	1 0 2 1 0	0 0 1 0 0	0 0 1 0 ?	0 1 ?
<i>Gymnotrachelus</i>	1 – 0 0 1	1 1 0 0 1	1 1 0 1 0	0 2 0
<i>Euseosteus</i>	1 0 2 0 1	1 1 0 1 0	0 0 ? 0 1	0 0 ?
<i>Microsteus</i>	1 0 2 0 1	1 1 0 1 0	0 1 1 0 1	0 0 ?
<i>Pachyosteus</i>	1 0 2 0 1	1 1 0 0 1	0 0 1 0 ?	0 0 0
<i>Rhinosteus</i>	1 0 2 0 1	1 1 0 0 1	1 1 1 0 ?	1 0 1
<i>Melaosteus</i>	? 0 ? 0 1	1 1 0 0 1	1 1 0 1 1	1 0 0
<i>Braunosteus</i>	? 1 1 0 0	0 0 0 0 0	0 0 1 0 ?	0 ? –
<i>Stenosteus angustopectus</i> sp. nov.	1 0 1 0 1	1 1 0 0 1	1 1 0 1 0	1 1 1
<i>Seleosteus brevis</i>	1 0 ? 0 1	? 1 0 0 1	1 1 0 ? ?	0 1 1

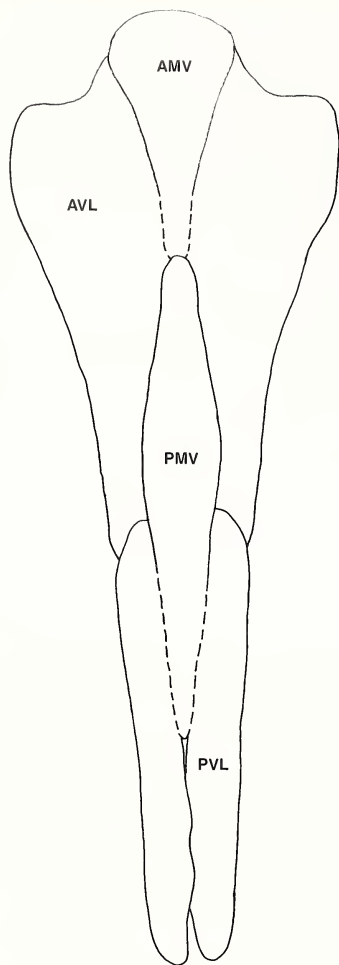


Figure 15. *Stenosteus angustopectus* sp. nov. A reconstruction of the ventral thoracic shield in dorsal view. Based on photographic tracings from CMNH 8042 (left AVL, left PVL, and PMV) and CMNH 8043 (AMV). Right elements are based on mirror images of the two left elements in CMNH 8042. The relationship of the AMV to neighboring bones is speculative due to a lack of visible overlap areas. Visible plate outlines are shown as solid lines. Visible reconstructed plate boundaries are shown as dashed lines.

Overlaps for the anterior lateral (oa.AL, Figure 14A), anterior dorsolateral (oa.ADL, Figure 14A), and posterior dorsolateral plates are present, although the latter is not distinct.

Interolateral (IL). The interolateral plate is missing in all the Cleveland Shale *Stenosteus* and *Selenosteus* specimens. The articular relationships between the branchial lamina of the anterior lateral plate, the anterior ventrolateral plate, and the anterior median plate remain obscure. There is no evidence, e.g., of overlap areas for direct anterior lateral plate articulation with the ventral shield, that would support the phylogenetic loss of the interolateral plate.

Anterior median ventral (AMV). An anterior median ventral plate is recognized in CMNH 8043 only and is exposed in internal view (Figures 14B, 15). The plate is triangular in outline with the base anterior (length/width at base = ca. 1.6). Bilateral shallow depressions on the internal surface (Figure 14B) may suggest the presence of overlap areas on the external surface (depressed during preservation).

Posterior median ventral (PMV). The posterior median ventral plate is incompletely preserved (Figures 15, 16A). The length of the preserved portion is ca. 73% of the total posterior ventrolateral plate length and ca. 59% of the medial length of the anterior ventrolateral plate. Externally, there are overlap areas for the anterior and posterior ventrolateral plates (oa.AVL and oa.PVL respectively, Figure 16A). Internally, a midline groove is present (gr, Figure 16C).

Anterior ventrolateral (AVL). The anterior ventrolateral plate (Figures 15, 16C) is elongate (median length/maximum width = ca. 3.6) with its greatest width anterior. The anterior ventrolateral plate tapers from its widest point to the posterior border with the lateral margin slightly concave. Anteriorly, there is a narrow medial process (pr., Figure 16C), which appears to extend the ventral shield well under the head.

Posterior ventrolateral (PVL). The posterior ventrolateral plate (Figures 15, 16B, C) is elongate, being over eight times longer than wide (length/width = ca. 8.4 in CMNH 8042). The ossification center is located approximately one-third the length of the plate from the plate's posterior border. An overlap area for the anterior ventrolateral plate (oa.AVL, Figure 16B) is present on the external surface and is located off-center with the distance to the medial edge being greater than that to the lateral edge.

Pectoral and Pelvic Fins, Axial Skeleton, and Neurocranium

The pelvic fins, axial skeleton, and neurocranium are not preserved. A single fragmentary scapulocoracoid (Figure 17) is preserved. Various, but poorly preserved perichondral ossifications are present. The scapulocoracoid (scap, Figure 17) is perichondrally ossified. The margin is incomplete; however, the scapulocoracoid appears to be taller than long. Muscle scars are restricted to the region of the pectoral crest. Numerous neurovascular canals are noted; however, homologies of individual canals are unclear.

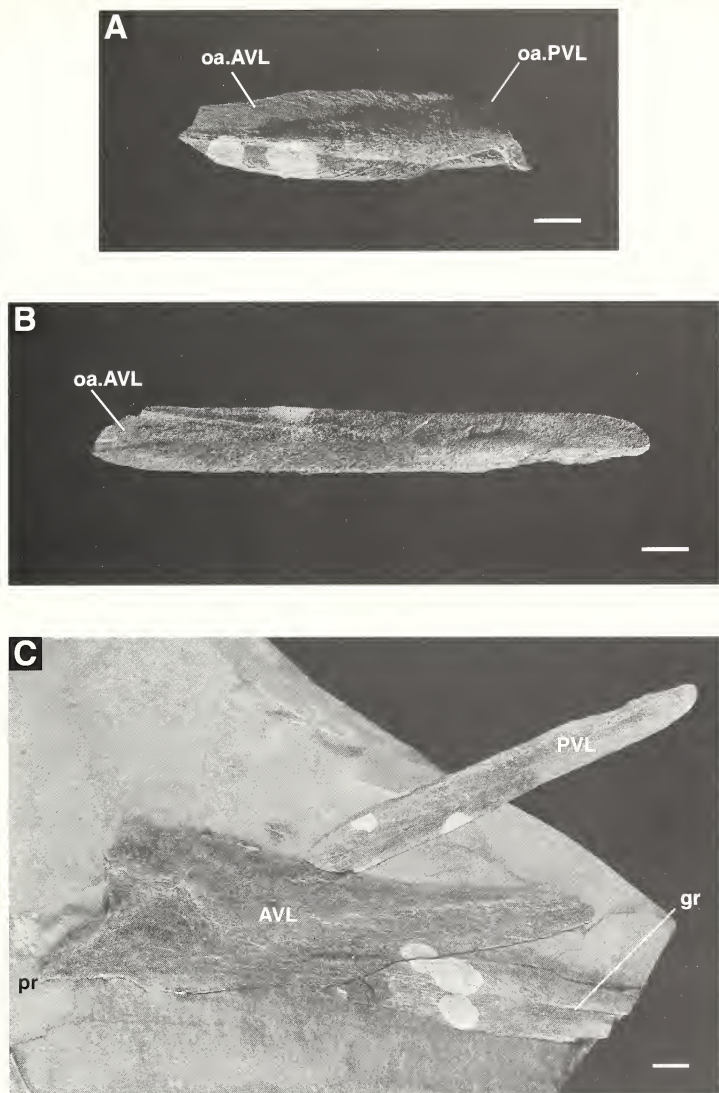


Figure 16. *Stenosteus angustopectus* sp. nov. (CMNH 8042). A, posterior median ventral plate in external view. B, left posterior ventrolateral plate in external view. C, right anterior ventrolateral, left posterior ventrolateral, and posterior median ventral plates in internal view. Scale bars = 1 cm.

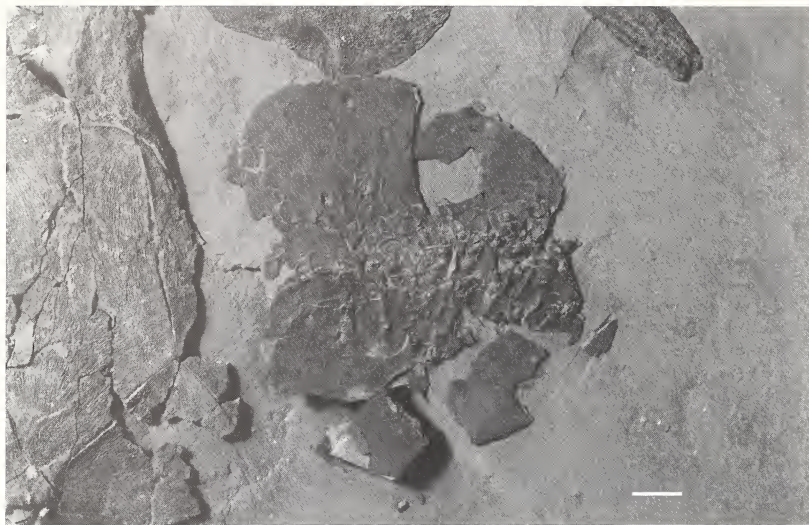


Figure 17. *Stenosteus angustopectus* sp. nov. Perichondrally ossified scapulothoracic (CMNH 8043) in lateral view. Scale bar = 1 cm.

Systematics Discussion

Phylogenetic analysis

Phylogenetic hypotheses are based on analyses using PAUP (v. 3.1, Swofford, 1993) which uses a parsimony argument to choose between alternative hypotheses of relationships (see Kluge, 1984, for a discussion of the application of parsimony to phylogenetic analyses). Character data and taxa used in the current analysis (Table 2) follow those of Lelièvre et al. (1987) and Carr (1994; *Gymnotrachelus*, *Melanosteus*, *Rhinosteus*, *Pachyosteus*, *Enseosteus*, *Microsteus*, *Braunosteus*, Brachydeiridae, and Trematosteidae) with *Stenosteus angustopectus* and *Selenosteus brevis* added to the study. Finally, diagnostic features of individual clades are based on a *a posteriori* analysis of character distributions (Patterson, 1982).

The current PAUP analysis gives ten equally parsimonious trees (individual treelengths = 31, consistency indices = 0.613), which provides an estimate of relationships based on currently published data, but fails to resolve completely the relationships of *Selenosteus* and *Stenosteus*. In contrast to Lelièvre et al. (1987), Carr (1994), and Gardiner and Miles (1994) the relationships within selenosteid arthrodires become ambiguous with the addition of *Selenosteus* and *Stenosteus* to the analysis. The utility of retaining

Selenosteus and *Stenosteus* as distinct genera is evaluated subjectively. Many of the diagnostic characters used to distinguish these two genera are missing in related forms thereby resulting in a lack of cladistic resolution. Parameters specified in PAUP include the branch and bound search option with all characters unordered and Trematosteidae set as the outgroup. The most parsimonious trees (minimal character transformations) and their strict consensus (a single tree showing those groups that are present in all eight trees) are retained for discussion.

The choice of outgroups has a minimal effect on the topology within Selenosteidae. All possible combinations of designated outgroups using either two or three non-selenosteid taxa (Trematosteidae, Brachydeiridae, and *Braunosteus*) differ only in the resolution of *Melanosteus*. When Trematosteidae is deleted from the analysis, *Melanosteus* is the sister taxon to an unresolved group (*Selenosteus*, *Selenosteus*, and *Gymnotrachelus*).

Characters 1–15 are taken from Carr (1994; characters 1–14 originally taken from Lelièvre et al., 1987) with three additional characters added to the current study. The characters are listed below:

1. Submarginal plate shape and orientation (modified from Lelièvre et al., 1987): elongate (0); short (1). Lelièvre et al. (1987, p. 17) consider the derived condition to be raised and reduced ("relevée et réduite"). The primitive condition is an elongate submarginal whose primary axis parallels the head shield margin (e.g., *Dunkleosteus*, Denison, 1978, fig. 69A). A shortened submarginal

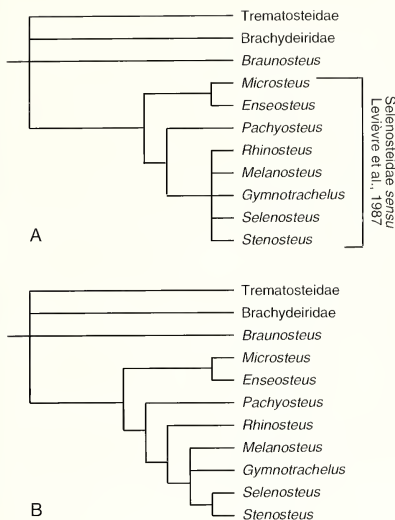


Figure 18. A, a strict consensus tree based on ten trees derived from PAUP (trees found with branch and bound search, treelength = 31, consistency index = 0.613). B, a tree representing the hypothesized relationships discussed in the text. A and B with Trematosteidae designated as the outgroup.

Trematosteus, *Cyrtosteus*, and *Brachyosteus* (the latter four taxa are members of the family Trematosteidae). It is not possible at present to distinguish between the fusion of the postnasal and preorbital plates from the loss of the postnasal plate and the independent development of an interfenestral process. The presence of two ossification centers would help to confirm the former hypothesis, although this information is not available in the current analysis.

- Marginal plate forms part of orbit margin (modified from Lelièvre et al., 1987): absent (0); restricted (1); unrestricted (2). This character represents a complex relationship between the head shield and cheek plates. The primitive condition is one where the marginal plate plays no part in forming the orbit border (e.g., *Dunkleosteus*, Denison, 1978, fig. 69A). The marginal plate, when excluded from the orbit or limited to a posterior recess, possesses a straight, convex, or minimally concave lateral edge. Two derived states, involving participation of the marginal plate in the orbit, are recognized. In forms such as *Microsteus* (Denison, 1978, fig. 76D), *Pachyosteus* (Denison, 1978, fig. 76C), *Rhinosteus* (Denison, 1978, fig. 76A), and brachydeirids (Denison, 1978, figs. 56B–D) the lateral edge of the marginal plate, in forming the posterior orbit margin, is strongly concave (the ventral margin is directed anteriorly in the latter two taxa). In all these forms and in *Enseosteus*, the suborbital plate is in close approximation with the marginal plate (a suborbital-marginal plate contact is seen in *Rhinosteus*, *Enseosteus*, and brachydeirids). A consequence of the above derived condition is a change in the head shield's outline along the posterior or ventrolateral corner (the corner or angle formed by a line from the para-articular process to the postmarginal plate and a line from the postmarginal plate to the orbit margin at the level of the marginal-postorbital plate contact). The primitive condition is a V-shaped ventrolateral corner. In the taxa above, possessing a marginal plate involvement in the orbit, the anterolateral edge of the ventrolateral corner possesses a distinct angulation resulting in the posterior orbit border paralleling, or nearly so, the posterolateral edge of the head shield corner (a condition representing an unrestricted involvement of the marginal plate in the orbit).

The marginal plate in *Stenosteus angustopectus* participates in the orbit margin, but is located within a posteriorly directed recess. The head shield retains a primitive V-shaped outline for the ventrolateral corner (a restricted involvement of the marginal plate in the orbit). A transitional condition between no involvement in the orbit margin and the marginal plate bordering an open posterior recess is seen in *Gymnotrachelus* where a small gap extends from the orbit between the head shield and cheek plates (Carr, 1994, p. 11, fig. 2B).

plate, only, is considered here as the derived condition since the character state of Lelièvre et al. (1987) implies both shortening and either elevation, rotation, or both. In *Gymnotrachelus* the submarginal is shortened but the primary axis remains parallel to the head shield margin, whereas, the submarginal appears to be rotated in forms such as *Rhinosteus* (Denison, 1978, fig. 76A) and *Brachyosteus* (Denison, 1978, fig. 74B). A distinct character state of rotation or elevation is not evaluated in the current analysis. To evaluate these features, information is required concerning the exact location of the ossification center which is not readily available.

- Postnasal plate fused to preorbital plate (Lelièvre et al., 1987): absent (0); present (1). Stensiö (1963, p. 342) interpreted the presence of an interfenestral process on the preorbital plate's dermal preorbital process (pr.if, Stensiö, 1963, fig. 103B) and its association with the course of the supraorbital sensory line groove as evidence for the fusion of the postnasal plate to the preorbital plate. He noted this condition in *Hadrosteus*, *Braunoosteus*, *Leioosteus*, *Erroneosteus*, *Belosteus*,

- Due to the complexity of these features, it is important in all cases to compare the relationship of the suborbital, posterior suborbital, and submarginal plates to clearly determine if the marginal plate is involved in the orbit margin. Among taxa where known, the internal supraorbital crista is restricted to the postorbital plate or as noted in this case extends only a limited distance onto the marginal plate. The posterior extent of this feature does not appear to be a good indicator of marginal plate involvement in the orbit border (see Stensiö, 1963, figs. 112A, B, 113A–C and Lelièvre et al. 1987, fig. 3).
4. Position of the preorbital-postorbital-central plate junction (Lelièvre et al., 1987): at a level over the anterior half of the orbit (0); posterior half of orbit (1).
 5. Angle formed by the postorbital and otic branches of the infraorbital sensory line grooves (Lelièvre et al., 1987): open (0); closed (1). Gardiner and Miles (1994) noted that an angle of less than 45° is restricted to *Selenosteus* and the European selenosteids with the condition in *Gymnotrachelus* being transitional. Carr (1994) reinterpreted the relationship of these sensory lines in *Gymnotrachelus*, noting an angle of ca. $30\text{--}40^\circ$.
 6. Length of cheek and head shield contact, independent of overlapping or fusion of these two dermal units (Lelièvre et al., 1987): long (0); short (1).
 7. Nature of inferognathal and posterior superognathal occlusal surfaces (Lelièvre et al., 1987): trenchant or rounded (0); denticulate (1).
 8. Posterior ventrolateral and posterior median plates (Lelièvre et al., 1987): present (0); absent (1).
 9. Position of the dermal articulation between the head and thoracic shields (modified from Lelièvre et al., 1987): dorsolateral (0); displaced ventrally (1).
 10. Dorsal process on the posterior superognathal plate (Lelièvre et al., 1987): present (0); absent (1).
 11. Form of the anterior lateral plate (Lelièvre et al., 1987): infraorbital region of plate short (0); infraorbital and postbranchial region elongate with the dorsal region narrow (1).
 12. Linguiform process on the suborbital plate (modified from Lelièvre et al., 1987): present (0); reduced (1). This character has been scored as in Lelièvre et al. (1987), although absence of a linguiform process is reinterpreted here as a reduction. The presence of a linguiform process may represent a plesiomorphic feature for the aspinothoracid arthrodires. Recognition of this process in lateral view may reflect the size of the subautopalatine crista (cr.sau, Figure 5B; Carr, 1991) and whether, when secondarily flattened during preservation, the process extends below the ventral external border of the suborbital plate. This crista is often thin and easily lost unless reinforced to form a contact face with the posterior superognathal as seen in *Dunkleosteus* and *Eastmanosteus calliaspis* (cf. PSG, Carr, 1991, fig. 7B).
 13. Overlap between the head and cheek dermal plates (Lelièvre et al., 1987): absent (0); present (1). Lelièvre (personal communication) reinterprets this character in *Melanosteus* as being absent (0), i.e., lacking an overlap, based on his interpretation of the lateral border of the head shield (see Lelièvre et al., 1987, fig. 3, Pl. 1 [figs. A–C]).
 14. Prehypophyseal region of parasphenoid plate elongate and stem-like (modified from Lelièvre et al., 1987): absent (0); present (1).
 15. Supraethmoid thickening (th.seth, Stensiö, 1963, figs. 113A, B): absent (0); present (1).
 16. Marginal and central plate contact: absent (0); present (1).
 17. Length ratio of parasagittal dimensions of preorbital and central plates (PrO/C; Denison, 1978): $x < 0.75$ (0); $0.75 < x < 1.25$ (1); $x > 1.25$ (2).
 18. In forms with a denticulate inferognathal, the nature of the denticle pattern: multiple rows (0); single fine row (1).
- Selenosteidae* Dean, 1901
- Dean (1901) originally described the family Selenosteidae, in which he included *Selenosteus*, *Stenosteus*, *Diplognatulus*, and possibly *Callognatulus*. He characterized the group based on the presence of a denticulate inferognathal, adsymphyseal denticles, large orbits, a lack of a postorbital process, a nuchal plate with a deep posterior embayment, a well-developed articulation between the head and thoracic shields, and the median dorsal plate shape with reduction of the carinal process and associated keel.
- Denison (1978) characterized the family by the presence of large orbits, long centrals (relative to preorbitals), short submarginal plates, and a large nuchal gap. He united within the family a number of European taxa (*Bramnosteus*, *Enseosteus*, *Microsteus*, *Pachyosteus*, and *Rhinosteus*) and North American taxa (*Gymnotrachelus*, *Paranylostoma*, *Selenosteus*, and *Stenosteus*). He noted differences between these two geographically separate faunas, although he did not provide a phylogenetic analysis.
- Lelièvre et al. (1987) added *Melanosteus* to the family and suggested that the brachydeirid arthrodires and Selenosteidae are sister taxa (Figure 18A). They excluded *Bramnosteus* from Selenosteidae and did not analyze *Paranylostoma*, *Selenosteus*, or *Stenosteus*. Gardiner and Miles (1994) also recognized a sister group relationship between *Gymnotrachelus* and European selenosteids (*Selenosteus* was not included in their analysis) although their proposed relationships among European selenosteids differ from that of Lelièvre et al. (1987). Following Lelièvre et al. (1987), Carr (1994) reevaluated the relationships of *Gymnotrachelus*, but excluded *Selenosteus* and *Stenosteus* from his analysis and considered the relationship of *Bramnosteus* unresolved.
- Lelièvre et al. (1987), Carr (1994; Figure 18), and Gardiner and Miles (1994) agree that Selenosteidae (exclud-

Table 3. The left column provides a summary of the plates identified and doubtful structures discussed by Dean (1901) for *Stenosteus glaber* AMNH 7313. Quotes are used to denote archaic terminology or specific phrases used by Dean. Page and plate references refer to discussions in Dean (1901). The right column provides a current interpretation of these structures. Caution should be taken in analyzing Dean’s original figures. The lithographic method employed by Dean reproduced the figures as mirror-images, a problem common to lithography (Griffiths, 1980, p. 101, figs. 89, 90).

Bones discussed by Dean (1901)	current interpretation
“Median occipital” (Nu) (p.89; Pl. IV, fig. 19)	present
Central (C) (p. 89; Pl. III, fig. 4)	present
Marginal (M) (p. 89; Pl. III, figs. 3c, 4)	present
“External occipital” (PNu) (p. 90; Pl. III, fig. 4)	present
Postorbital (PiO) (p. 90; Pl. III, figs. 3b, 4)	present
Preorbital (PrO) (p. 90; Pl. IV, fig 11)	present
Rostral (R) (p. 90; Pl. III, fig. 5)	= SM? (possible R can be seen between Psp and AL)
Pineal (P) (p. 90; Pl. IV, fig. 22)	= Psp
(?P, Pl. III, fig. 2)	= AMV?
“Mandible” (IG) (p. 91; Pl. IV, figs. 15, 17)	present
“Maxillaries” (PSG) (p. 91; Pl. IV, figs. 14, 14A)	present
“Premaxillaries” (ASG) (p. 92; Pl. IV, fig. 13)	present
Suborbital (SO) (p. 92; Pl. IV, figs. 12, 18)	present
Sclerotic (scler) (p. 92; Pl. III, figs. 7, 8, 10)	present (only 8 present)
Median dorsal (MD) absent (“no trace,” p. 93)	present (impression only, next to PMV)
Anterior dorsolateral (ADL) (p. 93; Pl. IV, fig. 16)	present
Posterior median ventral (PMV) (p. 93; Pl. IV, fig. 20)	present
Anterior median ventral (AMV) (p. 93)	present
(AVL) (p. 93; Pl. III, fig. 6)	? (possible AL)
(PVL) (p. 93; Pl. III, fig. 9)	? (possible AVL)
Doubtful plates discussed by Dean (1901)	current interpretation
Pl. III, fig. 3 (p. 90)	“a” = ?Marginal (due to presence of a short pmc)
	“b” = Postorbital
	“c” = Marginal
Pl. IV, fig. 22 (p. 90)	“Pi” = Parasphenoid
Pl. III, fig. 1 (p. 91)	= Pineal
Pl. III, fig. 2 (p. 91)	= AMV?
Plates not discussed by Dean (1901)	current interpretation
PL	present
PDL	present

ing *Braunosteus*) are characterized by: (1) enlarged orbits (character 5, Lelièvre et al., 1987; characterized by changes in the sensory line patterns associated with enlarged orbits), (2) a reduced cheek–head shield contact (character 6, Lelièvre et al., 1987), and (3) inferognathals and posterior superognathals possessing occlusal denticles (character 7, Lelièvre et al.,

1987). An anterior shift of the preorbital-postorbital-central plates triple junction unite Selenosteidae *sensu* Denison (1978), although the distribution of this character is equivocal when evaluating Selenosteidae *sensu* Lelièvre et al. (1987, Brachydeiridae as the sister group to Selenosteidae excluding *Braunosteus*). The distribution of short submarginal plates (a

Table 4. The left column provides a summary of the plates identified and doubtful structures discussed by Dean (1901) for *Selenosteus brevis* AMNH 7312. Quotes are used to denote archaic terminology or specific phrases used by Dean. Page and plate references refer to discussions in Dean (1901). The right column provides a current interpretation of these structures. Caution should be taken in analyzing Dean's original figures. The lithographic method employed by Dean reproduced the figures as mirror-images, a problem common to lithography (Griffiths, 1980, p. 101, figs. 89, 90).

Bones discussed by Dean (1901)	current interpretation
"Median occipital" (Nu) (p. 94; Pl. VI, fig. 33)	present
Central (C) (p. 94; Pl. VI, fig. 33)	present
Marginal (M) (p. 95; Pl. VI, fig. 33)	present
"External occipital" (PNu) (p. 95; Pl. VI, fig. 33)	present
Postorbital (PtO) (p. 96; Pl. VI, fig. 33)	present
Preorbital (PrO) (p. 96; fig. 1; Pl. VI, fig. 33)	present
Rostral (R) absent (p. 96)	absent
Pineal (P) absent (p. 96)	absent
"Mandible" (IG) (p. 96; Pl. VI, figs. 36, 37)	present
"Premaxillary" (ASG) absent (p. 94)	absent
"Maxillary" (PSG) absent (p. 94)	present
Suborbital (SO) (p. 97; Pl. VI, fig. 35)	present
Sclerotic (scler) (p. 97; Pl. VI, fig. 34)	present
Median dorsal (MD) (p. 97; Pl. V, fig. 23)	removed by Dean
Anterior dorsolateral (ADL) (p. 97; Pl. V, fig. 32)	present
Posterior dorsolateral (PDL) (p. 97; "not present ... unless ... shown in Pl. V, fig. 27")	absent?
Anterior ventrolateral (AVL) (p. 97; Pl. V, fig. 28)	present
Posterior ventrolateral (PVL) (p. 98; Pl. V, fig. 25)	present
Anterior median ventral (AMV) absent (p. 98)	absent
Posterior median ventral (PMV) (p. 98; Pl. V, fig. 26)	present
Integument (p. 99; Pl. V, fig. 24)	=Scapulocoracoid
(p. 99; Pl. V, fig. 31)	=perichondral ossification
Doubtful plates discussed by Dean (1901)	current interpretation
Pl. VI, fig. 33, X (p. 98) "preorbital"	?
Pl. VI, fig. 38 (p. 98) "clavicular" or "anterolateral"	=Anterior lateral
Pl. V, fig. 28A & Pl. V, fig. 30 (p. 98)	=Posterior suborbital
Pl. V, fig. 28B & Pl. V, fig. 29 (p. 98)	=Submarginal?
Pl. V, fig. 27 "interolateral" (p. 98)	=Posterior lateral
Plates not discussed by Dean (1901)	current interpretation
PL	present
PSO	present
SM	present
scapulocoracoid	present

Table 5. Characters suggesting distinctness of the genera *Selenosteus* and *Stenosteus*. The phylogenetic value of these features remains obscure due to missing data and the lack of information concerning original material in related taxa. A final resolution of the validity of these genera and their relationship within Selenosteidae is beyond the scope of the current study; however, the current analysis provides a basis for their retention.

<i>Selenosteus</i>	<i>Stenosteus glaber</i> and <i>S. angustopectus</i>
lacks a central-marginal plate contact	central-marginal contact present (Dean, 1901)
intricate marginal-paranuchal plate joint	simple plate joint (Dean, 1901)
reduced lateral paranuchal ala along the plate's posterior border	laterally expanded paranuchal ala
anterior paranuchal ala extends far forward	reduced anterior extension (Dean, 1901)
shallow concavity on ventral margin of the anterior dorso-lateral plate	accentuated concavity
concave posterior margin on the paranuchal lateral to the para-articular process	transverse posterior margin
accessory denticles along posterior aspect of the posterior superognathal plate	single row of denticles

selenosteid character used by Denison, 1978) has been shown to be a plesiomorphic feature of Selenosteidae (Lelièvre et al., 1987). The presence of a marginal-central plate contact (suggested selenosteid character, Dean, 1901) represents a derived feature within Selenosteidae (*Stenosteus*, *Rhinosteus*, and *Melanosteus*). The median dorsal plate shape and reduction of the carinal process and associated keel (Dean, 1901) additionally represent derived features within Selenosteidae seen in *Gymnotrachelus*, *Selenosteus brevis*, and *Stenosteus angustopectus*.

The confusion concerning family membership and the exclusion of taxa in analyses is a result, in part, of a lack of morphological information for various North American taxa. Additionally, *Selenosteus* and *Stenosteus* have not

been reevaluated since Dean's (1901) original report leaving the published descriptions inadequate and in error. The description of *Stenosteus angustopectus* provides useful comparative material to reevaluate the type specimens of *Selenosteus brevis* and *Stenosteus glaber*. Tables 3 and 4 provide a current reinterpretation of the individual bones discussed and figured by Dean (1901).

Within Selenosteidae (Figure 18B), *Selenosteus* and *Stenosteus* are united by the presence of a single row of finely spaced denticles along the inferognathal occlusal surface (Character 18) and a reduction in the central plate length relative to the preorbital plate (PrO/C ratio is subequal, Character 17). The first character above represents a subjective comparison based on figures of potential sister and outgroup taxa (i.e., *Rhinosteus*, Stensiö, 1963, Pl. 20 [fig. 1]; *Gymnotrachelus*, Carr, 1994, fig. 9; *Melanosteus*, Lelièvre, personal communication). The second character is distinct from the plesiomorphic state of elongate central plates with *Gymnotrachelus* representing a derived condition of elongate preorbital plates. The polarity of character transformations from the plesiomorphic state (elongate central plates) to the two derived states (subequal central and preorbital plates and elongate preorbital plates) is unclear.

Carr (1994, fig. 13) united *Melanosteus* and *Gymnotrachelus* based on the presence of a stem-like prehypophyseal region of the parasphenoid plate. This feature is also present in *Stenosteus angustopectus*, but unknown in *Stenosteus glaber* and *Selenosteus*. The presence of this process along with the relationship between *Selenosteus* and *Stenosteus* suggests a close relationship between these later two taxa, *Melanosteus*, and *Gymnotrachelus* (Figure 18). These four taxa additionally share a loose connection between the dermal cheek and head shield (Character 13); however, the exact nature of the relationships among these taxa remains unresolved.

Selenosteus and *Stenosteus*

Dean (1901) recognized AMNH 7312 and AMNH 7313 as two distinct genera, *Selenosteus* and *Stenosteus* respectively. He stated (p. 100) that "in differentiating *Stenosteus* as a genus stress has been laid upon its unlikeness to *Selenosteus* in the elements figured in Pl. III, figures 4, 6, 9, and in Pl. IV, figures 11, 21, 22." Dean's (1901) plate interpretations are updated in Tables 3 and 4 with Table 5 providing a summary of differences between these two genera. The phylogenetic value of these differences remains obscure due to missing data and the lack of published information concerning specific characters in related taxa. A final resolution of the validity of these genera and their relationship within Selenosteidae is beyond the scope of the current study.

Stenosteus is characterized by the presence of (1) a narrow laterally extending ala on the paranuchal plate along its posterior border, (2) a reduced anterior extension of the anteromedial part of the paranuchal plate (Dean, 1901), and

(3) a developed concave ventral border of the anterior dorso-lateral plate. *Selenosteus* is characterized by (1) a convoluted suture between the marginal and paranuchal plates (Dean, 1901), (2) a concavity along the posterior margin of the paranuchal plate lateral to the para-articular process, and (3) the presence of accessory denticles along the posterior aspect of the posterior superognathal plate.

Conclusion

A new selenosteoid arthrodire, *Stenosteus angustopectus*, is described from the Cleveland Shale of northern Ohio, U.S.A. Characterizing *Stenosteus angustopectus* are: (1) long and narrow posterior ventrolateral plates, (2) a narrow median process on the anterior ventrolateral plate, (3) a tongue-in-groove joint between the anterior lateral and anterior dorso-lateral plates, (4) a posterodorsal process on the suborbital plate, and (5) a posterior superognathal plate lamina that posteriorly is rotated 90°. This material provides the basis for reevaluating Dean's (1901) original descriptions for *Stenosteus glaber* and *Selenosteus brevis*. Dean's figures and identifications of individual bones are reinterpreted with an update provided in Tables 3 and 4. The taxon Selenosteidae is retained *sensu* Lelièvre et al. (1987) and is diagnosed by the presence of large orbits with associated shifts in the sensory line grooves around the orbit and reduction in the contact between the cheek and head shield, and finally by the presence of a denticulate inferognathal occlusal surface. Additional published characters used to unite Selenosteidae are either equivocal, plesiomorphic, or derived relative to the family (respectively: Pro/C ratio, submarginal plate shape, and marginal-ventral plate contact and median dorsal plate shape). *Selenosteus* and *Stenosteus* are retained as distinct genera and united as sister taxa. Uniting these taxa are the pattern of denticulation along the inferognathal and a reduction of the relative length of the central plates. A number of characters distinguish *Selenosteus* and *Stenosteus* (summarized in Table 5), although their phylogenetic value is obscured by missing data and incomplete published accounts of related taxa. Finally, diagnoses are provided for *Selenosteus* and *Stenosteus* based on current knowledge of the taxa analyzed in this study.

It is important to the understanding of aspinothoracid phylogenetic relationships that North American taxa continue to be reanalyzed. The Cleveland Shale fauna is a key element since the recovery of a wealth of material during the Interstate 71 Paleontological Salvage Project provides both new taxa and important comparative material for the analysis of poorly known forms. It is equally important to reevaluate much of the Wildungen material discussed and described by Stensiö (e.g., Stensiö, 1963) in light of current work. At present, the state of published descriptions limits this process.

The current work on the Cleveland Shale fauna and the description of a new species of *Stenosteus* helps to resolve a number of questions concerning related taxa and provides a

step toward understanding the phylogenetic relationships among aspinothoracid arthrodires. Continuing work on this fauna should prove to be valuable.

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Abbreviations Used in Text and Figures

a.Au	depression for autopalatine	f.lv	elongate fossa for levator muscle of head
ADL	anterior dorsolateral plate	gr	groove
adsym.dent	asymphyseal denticles	IG	inferognathal
AL	anterior lateral plate	ioc.ot	otic branch of infraorbital sensory line groove
AMV	anterior median ventral plate	ioc.pt	postorbital branch of infraorbital sensory line groove
ant	anterior	ioc.sb	suborbital branch of infraorbital sensory line groove
a.po	postautopalatine crista	kd	glenoid condyle
AVL	anterior ventrolateral plate	laf	lateral articular fossa
av.w	anteroventral wing	lam	lamina
C	central plate	lam.br	branchial lamina of AL plate
cf.PrO	contact face for preorbital plate	lc	main lateral line
cr.po	postocular crista	M	marginal plate
cr.pr	carinal process	MD	median dorsal plate
cr.pso	postocular crista	n	notch
cr.sau	subautopalatine crista	Nu	nuchal plate
cr.so	subocular crista	oa.ADL	overlap area for anterior dorsal lateral plate
csc	central sensory line groove	oa.AL	overlap area for anterior lateral plate
d.end.e	external opening for the endolymphatic	oa.AVL	overlap area for anterior ventrolateral plate
f.bhy	paired buccohypophysial foramina	oa.M	overlap area for marginal plate
		oa.MD	overlap area for median dorsal plate
		oa.PL	overlap area for posterior lateral plate
		oa.PNu	overlap area for paranuchal plate
		oa.PVL	overlap area for posterior ventrolateral plate
		oa.SM	overlap area for submarginal plate
		oa.SO	overlap area for suborbital plate
		P	pineal plate
		pap	occipital para-articular process
		PDL	posterior dorsolateral plate
		PL	posterolateral plate
		PM	postmarginal plate
		pmc	postmarginal sensory line groove
		PMV	posterior median ventral plate
		PNu	paranuchal plate
		p.pr	median posterior process
		pr	process
		pre.reg	prehypophysial region
		PrO	preorbital plate
		pr.pv	posteroventral process
		pr.sg	subglenoid process
		PSO	postsuborbital plate
		Pto	postorbital plate
		PVL	posterior ventrolateral plate
		Qu	position of quadrate
		R	rostral plate
		rec.pr.sv	recess for the supravagal process of the neurocranium
		sh	shelf
		SM	submarginal plate
		SO	suborbital plate
		soa	subobstantic area
		soc	supraorbital sensory canal groove

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PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

PRESENTATION OF THE AWARD

MARY LOU FERBERT

*Trustee, The Cleveland Museum of Natural History
1 Wade Oval Drive, University Circle
Cleveland, Ohio 44106-1767*

Roger Tory Peterson, on behalf of the Board of Trustees of The Cleveland Museum of Natural History, it is indeed a privilege to have you with us tonight. I have the singular honor of introducing you as this year's recipient of the David S. Ingalls, Jr. Award for Excellence.

The Museum's and Dr. Peterson's relationship goes back many, many years, at least 63 years, and we can document this. You will find on exhibit outside the auditorium correspondence from the early 1930s between Roger Tory Peterson and Dr. Oberholser and John Aldrich—both Museum staff members—with regard to an opening in the bird department for which Roger Tory Peterson was considering applying. Noting the year, 1931, and the economic climate—depression—I'm sure an opening-level position salary would not have been very attractive, but the mutual respect between our award recipient and these two men is obvious in the letters.

I would like to quote a sentence in one of his letters from Camp Chewonki, Wiscasset, Maine, to Dr. Oberholser, dated August 12, 1931: "I am an art student at present and it is my hope to give the others of this rising group of young bird artists a run for their money."

In 1940 Dr. Peterson provided all the illustrations for The Cleveland Museum of Natural History publication, *A Field Key to Our Common Birds*, written by Irene Rorimer. Dr. Peterson created 44 tempera drawings and 35 ink drawings for the booklet. This artwork, a part of the Museum's fine arts collection, is also hung outside this auditorium.

In 1981 the Museum hosted "Bird Art," a juried exhibition sponsored by the Leigh Yawkey Woodson Art Museum of Wausau, Wisconsin. Roger Tory Peterson was the honored guest and program speaker at the opening. Over 850 people crowded the auditorium to hear him. Dr. Peterson's fourth edition of his *Field Guide to the Birds* had come out in 1980, and he graciously consented to a reception and book-signing following the program. Many of us here tonight remember queuing up to collect his autograph in the new fourth edition as well as in older copies. Frannie Newell, a Museum volunteer, had him sign her mother's copy of the first edition that had been Frannie's bird primer as a child.

The following morning Dr. Peterson met with the Future Scientists and the exchange was so exhilarating and stimulating for all participants, it was very hard to pry him away. I feel it's safe to say that motivating a

*On May 20, 1994, the David S. Ingalls, Jr. Award for Excellence was presented to Roger Tory Peterson. The text of Mary Lou Ferbert's speech on that occasion is printed here in a slightly shortened version. Roger Tory Peterson's remarks are excerpted, with his permission, from more extensive notes used during his acceptance speech.

group of kids provides him as much enjoyment as any of his mega-accomplishments.

And, continuing our relationship with this gifted man, tonight he is again with us and he is about to receive the David S. Ingalls, Jr. Award for Excellence. Our award recipient was born in Jamestown, New York. When he was eleven he came upon a flicker asleep on a tree trunk. He assumed it was dead. Being inquisitive, he investigated. Then he witnessed it suddenly burst into life and fly off. It was a magical, mystifying experience. It triggered a life's journey.

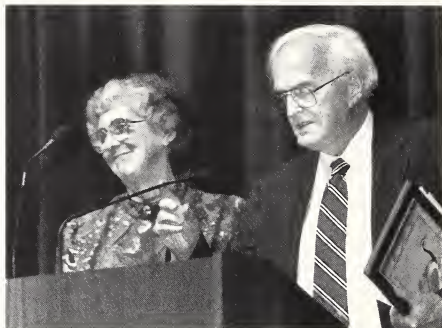
While still a teenager, he dazzled the elder naturalists with his broad knowledge of natural history gained through direct field experience and study. His academic training was in painting, five years at the Art Students League and the National Academy of Design in New York. Of course, during his New York tenure he was an eager visitor to the American Museum of Natural History where he could compare and contrast beaks and feet and plumage to his heart's content.

As a young man he spent several years teaching natural science at summer camps in Maine. At Rivers Country Day School in Brookline, Massachusetts, he taught art and science. While teaching there William Vogt, the first editor of Audubon magazine, persuaded him to write and illustrate a pocket-sized guide for bird watchers. Four publishers rejected the manuscript, but Houghton Mifflin printed a conservative 2,000 copies of *A Field Guide to the Birds* in 1934. It sold out within a week. A career was launched and he became a legend in his field overnight.

Dr. Peterson's matchless paintings, combined with the Peterson identification system, revolutionized and simplified field observation, giving the layperson the opportunity to become adept at identifying birds in a much shorter period of time—a few years as opposed to a lifetime. Sixty years and over five million copies later, it is still the standard against which all other field guides are measured. I would venture to say, it's a staple in home libraries. How many people in the audience own at least one Peterson field guide?

It is impossible to list all of his accomplishments. The field guide series now includes more than 60 titles. In addition to acting as editor of this series, Roger Tory Peterson has written, illustrated, and edited over 15 other books, many of which have sold millions of copies. And they have been translated into as many as 12 languages. His original paintings and limited edition prints have appeared in over 50 private exhibitions and public museums around the country. In April 1984 the Smithsonian Institution mounted an exhibit of Peterson's paintings in honor of the 50th anniversary of *A Field Guide to the Birds*.

I would like to read a portion of the remarks by S. Dillon Ripley, Secretary of the Smithsonian Institution, on that occasion: "Roger Tory Peterson — more than any other person of our time — you epitomize the field naturalist in the public mind. With genius and simplicity, talent and dedica-



Museum Director Dr. J. Mary Taylor and Roger Tory Peterson, May 20, 1994.

tion, you persisted in an idea and fashioned a small book that became a giant and a first in its class. Overnight, *A Field Guide to the Birds* revolutionized the field...."

Dr. Peterson is the recipient of 22 honorary degrees from American universities in the diverse disciplines of art, science, humanities, and letters. President Carter bestowed the Presidential Medal of Freedom on him in 1980. This medal is the highest honor a civilian can be awarded in the United States. Time does not permit me to list his many other awards.

Roger Tory Peterson, you are teacher, artist, ornithologist, author, editor, field naturalist, conservationist, environmentalist, photographer, cinematographer, and lecturer. You are a national treasure. Invertebrate traveler would also describe you. You have seen more than 5,000 birds, over half the world's species, and you are still going! In 1992 you, with your wife Ginny, completed your 18th trip to Antarctica. You have observed and photographed birds on every continent, and you have photographed all species of flamingos and penguins in their natural habitats, a unique accomplishment. Your abiding love for photography is less well-known and overshadowed by your painting reputation, but photography is a significant part of your oeuvre.

In the 1970s when our honored guest was approaching his 70s, with many lifetimes of productive work to his credit, Dr. Peterson embarked on a new project, the Roger Tory Peterson Institute of Natural History, in Jamestown, New York. In August of last year, this dream became a reality as the new Roger Tory Peterson Institute building was dedicated.

Dr. Peterson spawned a national pastime. He has led tens of millions of people outdoors with the Peterson field guides in their pockets to experience the natural world. I think all of us contemplate immortality. You, sir, have achieved it through your gift to humankind. We thank you.

REPLY

ROGER TORY PETERSON

125 Neck Road

Old Lyme, Connecticut 06371

Ladies and gentlemen, members and friends of The Cleveland Museum, it is a moving experience to be with you today and to receive the David S. Ingalls, Jr. Award. Over the years I have enjoyed my many contacts with the birders in and around the Cleveland area. Many of them are no longer with us. Recently a young person asked me if I ever knew Audubon. "Good heavens," I replied, "I am not that old."

Birds, the most beautiful, the most dynamic and most observable of all wild things, have been the focus of my life since I was a boy of eleven. For more than 70 years they have occupied my daily thoughts, filled my dreams, and dominated my reading. But what, you may wonder, happened when I was eleven that changed me from a rebellious youngster to an obsessed bird watcher?

It was because of a teacher I had in the seventh grade. Miss Hornbeck, a red-haired lady about 30 years old, organized a junior Audubon Club, and we each received ten leaflets about birds, each with a color plate of the bird and an outline drawing to color. But coloring in the outlines was not much of an artistic challenge, so Miss Hornbeck provided each of us with a little box of watercolors and a brush and had us copy from color plates by Fuertes. She gave me the blue jay to copy. I thought I did OK, but when our drawings were put up on the blackboard she credited my blue jay to Edith, the girl who sat across the aisle. I was very upset. Realizing her mistake, Miss Hornbeck soon put things straight. I have often wondered what became of Edith.

Because the blue jay was my first attempt at bird drawing, the blue jay remains one of my favorites. But the incident that really hooked me on birds for life took place the following weekend. It was a Saturday in April, 1920, 70 years ago. A classmate, Carl Hammerstrom, who lived up the street, and I crossed the railroad tracks and climbed Swede Hill to explore new territory. As we entered a grove near the crest of the hill we spotted a bundle of brown feathers clinging to the trunk of a tree. It was a flicker, asleep, with its bill and face tucked under the feathers of its back. It was probably resting from migration, but I thought it was dead. I touched it on the back, and instantly this inert bundle of feathers sprang to life, looked to me with wild eyes, then dashed away in a flash of gold. It was like resurrection. What had seemed dead was very much alive. Ever since

then, birds have seemed to me to be the most vivid expression of life.

I like to think of my own contribution to the conservation-environmental movement as one of interpreter and opinion-maker through my writing and my painting. It started with my field guides—a visual system—putting names to things—employing shape, patterns, and field marks. My field guides were a useful invention, but to do their job the drawings are rather formal and schematic, a different "art form," if you will. To have done them otherwise would have compromised the purpose for which they were intended—simplification—a short cut to field identification so that a person might soon have some competence and then go on to behavior, ecology, artistic portrayal, environmental activism, or whatever. The "Peterson system," as my method has been called, is a visual one consistent with field birding. The system is based on patternistic drawings with arrows that pinpoint field marks as seen at a distance. These rather formal illustrations and the direct comparisons between similar-looking species are the core of the system, unlike the more traditional bird portraiture found in most other bird books. However, I leaned a bit more toward portraiture in the fourth edition while trying not to lose the basic abstraction....

My wife Ginny and I are still working on the new eastern field guide. (It will be the 6th edition.) She is working on the maps and I still have a few color plates to work on; then I will be back to my real painting. The recent things that I have done as limited edition prints (for Mill Pond Press) are a transition stage—most of them fall into the category of decorative portraiture, delineation in the Audubon tradition. Now I intend to paint more expansively—to get back into oils and canvas again, to play with mood and color and light. To paint more sensuously, the kind of painting for which I was originally trained at the Art Students League and the National Academy under such Masters as Kimon Nikolaides, John Sloan, and Vincent Dumond, Raymond D. Neilson and Edmund Dickinson. That was good training because wildlife painting cannot go too far from realism without risking affectation. Now I intend to indulge myself and return to a more painterly kind of painting—living birds with three-dimensional activity, movement in space, and, of course, with some biological comment....

Thank you very much.

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INVERTEBRATE PALEONTOLOGY

*REMAINS OF ARTHROPLEURA, A GIGANTIC MYRIAPOD ARTHROPOD,
FROM THE PENNSYLVANIAN OF OHIO AND PENNSYLVANIA*

Joseph T. Hannibal

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VERTEBRATE PALEONTOLOGY

*FOSSIL YAK (BOS GRUNNIENS: ARTIODACTYLA, MAMMALIA)
FROM THE HIMALAYAS OF PAKISTAN*

J. G. M. Thewissen, S. T. Hussain, S. I. Madar, E. Ganz, M. Arif and H. Hussain

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REMAINS OF *ARTHROPLEURA*, A GIGANTIC MYRIAPOD ARTHROPOD, FROM THE PENNSYLVANIAN OF OHIO AND PENNSYLVANIA

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ABSTRACT

Fossils attributed to *Arthropleura* Jordan, a genus of gigantic myriapod arthropod, are described from lower Conemaugh (?Missourian) rocks at the 7-11 site, a strip mine in Columbiana County, Ohio, and from Allegheny (Desmoinesian) rocks at Cammelton, Beaver County, Pennsylvania. The specimens from these localities consist primarily of rosette and B plates, body parts that would have been closely associated with limbs of the organism in life. The Ohio specimen represents an animal whose length exceeded 1.5 m; the Pennsylvania specimen probably represents a smaller, but still large, individual. The Ohio arthropleurid is probably conspecific with *Arthropleura cristata* Richardson, which belongs to the Desmoinesian Mazon Creek, Illinois, fauna. The specimen from Pennsylvania may also belong to the same species.

Introduction

Arthropleurids are a group of myriapod animals that includes the largest known terrestrial arthropods. Fossils of arthropleurids are known from Upper Silurian (Pridoli) through at least Upper Carboniferous (Stephanian) rocks (Shear and Kukalová-Peck, 1990; Ross and Briggs, 1993; Briggs and Almond, 1994; Shear and Selden, 1995). The largest and most common genus of arthropleurid is *Arthropleura* Jordan, which is usually cited as being restricted to the Carboniferous. Barthel and Schneider (*in* Barthel and Rössler, 1995, p. 7), however, have recently noted an occurrence in the Lower Rotliegend which may extend the range of *Arthropleura* into the Lower Permian. About 10 species of *Arthropleura* have been described from Europe (Almond, 1985) and two have been described from North America. Many of the species of *Arthropleura* were of gigantic size.

Body fossils referable to the genus *Arthropleura* have been described from a number of countries in western and central Europe, including Britain, France (Briggs and Almond, 1994), the Netherlands and Germany (Hahn et al., 1986), and the Czech Republic (Spinár, 1960), as well as Kazakhstan (Novozhilov, 1962). These occurrences range from the Westphalian A (Hahn et al., 1986) to at least the Stephanian (Briggs and Almond, 1994; but also see Barthel and Schneider *in* Barthel and Rössler, 1995). Despite the widespread distribution of body fossils of *Arthropleura* in Europe, body fossils have previously been described from only two localities in North America: the Mazon Creek region, Illinois (Westphalian D; Desmoinesian in Midcontinent terminology), and Springhill, Nova Scotia (Westphalian B; Atokan in Midcontinent terminology).

Trackways produced by *Arthropleura* have been recorded from Fife, Scotland (Viséan; Pearson, 1992); Arran, Scotland (Namurian); Montceau-les-Mines, France (Stephanian B; Briggs and Almond, 1994); Joggins, Nova Scotia (Westphalian B; Ferguson, 1975); and Gardner Creek, New Brunswick (Westphalian A or B; Briggs et al., 1984). Based on the occurrence of body and trace fossils, the stratigraphic range of *Arthropleura* is Namurian A (Viséan) to at least the Stephanian (Ross and Briggs, 1993; Briggs and Almond, 1994). The paleoecology of *Arthropleura* has been discussed in a number of papers, including Rolfe (1985) and Shear and Kukalová-Peck (1990).

The purpose of this paper is to describe two specimens of *Arthropleura* from the Appalachian Basin of North America and to briefly review other North American reports of the genus.

In 1956, Richardson described specimens of *Arthropleura* from the Mazon Creek, Illinois, fauna. He subsequently (1959) named a new species, *A. cristata*, from the Mazon Creek area, designating a specimen con-



Figure 1. North American localities from which body fossils of *Arthropleura* and trace fossils thought to have been produced by *Arthropleura* are known. 1. Mazon Creek region, Illinois, body fossils described by Richardson (1956, 1959). 2. 7-11 Mine, northeastern Ohio, occurrence first noted by McComas and Mapes (1985), body fossil described in this paper. 3. Cannelton, Pennsylvania, body fossil described in this paper. 4. Gardner Creek, New Brunswick, *Diplichnites*, a trackway ascribed to *Arthropleura*, described by Briggs et al. (1984). 5. Springhill, Nova Scotia, body fossil described by Copeland (1957); and Joggins, Nova Scotia, trackways noted by Ferguson (1975).

sisting of a partial paratergal fold (FMNH PE 5262), as the holotype. Based on size and geographic association, Richardson also referred previously described arthropleurid material, consisting of a limb (now USNM 439582) and portions of plates (FMNH PE 9303 and 9304) that would have been associated with limbs in life, from the Mazon Creek area to that same species. While it is certainly likely that all these Mazon Creek specimens are conspecific, proof awaits a specimen that bears well-preserved, associated limb and tergal material. Nevertheless, Richardson's reasoning for referral of all of this material to the same species is plausible; therefore, I am following his conception of the species.

In 1957, Copeland described and illustrated (p. 52; Pl. XV, fig. 2) a small (23 mm long) specimen of *Arthropleura* from Springhill, Nova Scotia. The specimen, consisting of portions of several tergites in dorsal view, was originally assigned to the genus *Annyulysipes* Scudder. Rolfe (1969, p. R617) subsequently corrected the generic identification, assigning it to the genus *Arthropleura*. Judged by Copeland's photograph and description of this specimen, its spinosity and tuberculation is somewhat similar to that of *A. cristata*. The incompleteness and large size of the holotype of *A. cristata*, however, hampers com-

Series		<i>Arthropleura</i> localities
PENN-SYLVANIAN	Virgilian	
	Missourian	● (?) 7-11 Mine, Ohio
	Desmoinesian	● Cannellton, Pennsylvania & Mazon Creek, Illinois
	Atokan	● Springhill, Nova Scotia
	Morrowan	

Figure 2. Chart showing stratigraphic distribution of body fossils of *Arthropleura* found in North America. Midcontinent (USA) terminology is used.

parison between the Mazon Creek and Nova Scotia forms.

Schultze (1972, p. 94) noted the occurrence of a fragmentary fossil tentatively identified as *Arthropleura* from the upper part of the Escuminac Formation (Upper Devonian) of the Escuminac area, Quebec. This fragment does not belong to an arthropleurid (Rolfé in Jeram, 1996, p. 110), but instead is a part of an unidentified chelicerate. *Eoarthropleura* is found, however, on the New Brunswick side of Escuminac Bay, in what may be Emsian strata (Shear and Selden, 1995, p. 373).

Arthropleura has previously been noted as occurring in Ohio at the 7-11 Mine (McComas and Mapes, 1988) and arthropleurid remains have been noted as possibly occurring at Linton, Ohio (Hook and Baird, 1988, p. 57). The 7-11 material is described here. The Linton occurrence, which has been cited subsequently in comprehensive lists of taxa found at Carboniferous sites, e.g., by Schultze and Mapes (1992, appendix 1), is probably not valid. Donald Baird, who has studied Linton fossils over a 40-year period, has never seen an authentic specimen of *Arthropleura* from that site, and feels that the report of *Arthropleura* at Linton may have been based on a misidentification (D. Baird, personal communication, 1993). North American localities with verifiable occurrences of body or trace fossils which can be ascribed to *Arthropleura* are plotted on Figure 1. The stratigraphic distribution of body fossils of *Arthropleura* found in North America is shown in Figure 2.

Terminology used here follows that of Rolfé (1969, see especially fig. 390), which is based on that of previous workers, including Waterlot (1934). As used here, the terms plate and lobe, and the lettering of the lobes of the rosette plate, have no particular functional implication. Abbreviations used in this paper are: CaMNH Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; YPM, Yale Peabody Museum; USNM, U.S. National Museum of Natural History.

Systematic Paleontology

Class ARTHROPLEURIDEA Waterlot, 1934 (*nom. correct.*)

Order ARTHROPLEURIDA Waterlot, 1934

Remarks

Rolfé (1969) revised the higher order classification of this group, placing Guthörl's (1934) order Gigantopleurida in synonymy with Waterlot's (1934) order Arthropleurida. However, Rolfé considered the Arthropleurida to be a class. Later, Störmer (1976, p. 90) placed the order Arthropleurida in the identically spelled class Arthropleurida. Subsequently Hahn et al. (1986) placed the order Arthropleurida in the identically spelled subclass Arthropleurida. More recently, Shear and Selden (1995) named a new order of arthropleurid, the Eoarthropleurida, and used the name Arthropleurida at class level. The name Arthropleurida is here used to designate the order, retaining Waterlot's (1934) designation at its original ordinal level. A slightly different term, Arthropleuridea, is used at the class level to avoid confusion (this emendation has been suggested by William Shear, personal communication, 1996).

Family ARTHROPLEURIDAE Zittel, 1885

Genus ARTHROPLEURA Jordan in Jordan & Meyer, 1854

Diagnosis

Small to large multisegmented arthropods with approximately 30 wide tergites. Numerous limbs, each consisting of 8-10 segments. Several plates, including multilobed rosette plates, located at base of legs.

Discussion

The nomenclatorial histories of the genus and the type species were reviewed by Hahn et al. (1986).

ARTHROPLEURA CRISTATA Richardson, 1959

Figures 3-5

Arthropleura sp. RICHARDSON, 1956, p. 72-76, fig. 39, 40; ROLFÉ & INGHAM, 1967, Pl. 1, fig. 7; ROLFÉ, 1969, figs. 391b-c.

Arthropleura cristata RICHARDSON, 1959, p. 79, figs. 42-43; LANGFORD, 1963, p. 19, figs. 22-24.

Material studied

CaMNH 33853, consisting of a rosette plate with attached B plate as well as a smaller (?) limb fragment, both closely associated on the same slab. Counterpart, consisting primarily of a mold of this material, present on matching slab. Collected by Gregory A. McComas from the 7-11 Mine, a strip mine in Columbiana County, Ohio (Carnegie Museum stratigraphic locality [SL] no. 2087). This locality is located 1.1 km north of the intersection of

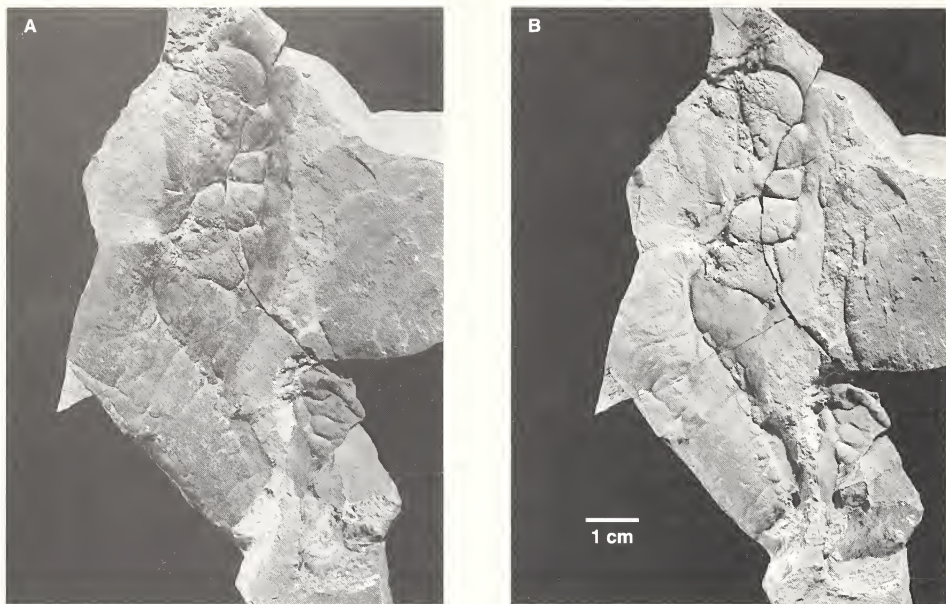


Figure 3. *Arthropleura cristata* Richardson, CaMNH 33853, collected at the 7-11 Mine, northeastern Ohio, by Mr. Gregory McComas. A, specimen unwhitened; B, specimen whitened. Specimen consists of a rosette plate with an attached B plate as well as a smaller (?) limb (appendage) fragment.

Ohio routes 7 and 11. The specimen, preserved in medium dark gray shale, was found as float, but G. McComas (personal communication) has been able to trace the lithology to a dark shale ("Brush Creek") in a high wall in the mine. The "Brush Creek" is lower Conemaugh (?Missourian).

Plant fragments, including *Lepidophyllum* sp. (S. Chitale, Cleveland Museum of Natural History, personal communication, 1996), and small conchostracans are also found on the slab containing the arthropleurid. Walchian conifers, ostracods, insects, and other arthropods are found in the dark shale at this locality; additional information on the locality and its flora and fauna is given in McComas (1988) and McComas and Mapes (1988).

Description

Right B plate and attached rosette plate (Figures 3, 4) very large for genus. Length of entire preserved section 95 mm. B plate (left side of Figures 3A&B, 4) 72 mm long, subrectangular, with straight, rounded posterior edge; bulbous extension of B plate abuts posterior border of rosette plate; row of large but subtle tubercles arranged in linear

fashion, beginning close to triple intersection of B plate with I lobe and anterior border of rosette plate, and extending toward proximal margin of B plate (Figures 3A&B, 4; left side of Figure 5); several wrinkles extend posteriad from between tubercles and from intersection of I lobe and B plate, otherwise smooth to very low tuberculation. Length of anterior border of rosette plate (=length of entire preserved section of rosette plate) 71.6 mm. Rosette plate (Figures 3, 4) with prominent, wide, anterior and posterior borders and five major lobes. Anterior border mostly smooth, posterior border with small tubercles. I lobe subtriangular, 18.7 mm long measured along long axis and about 15 mm wide at widest point, with corner abutting anterior border of B plate produced distally; several large tubercles located along border with B plate, remainder subtly wrinkled. C lobe irregularly five-sided, 14.4 mm long and 10.5 mm wide, covered with fine tubercles. Triangular lobe, 7.9 mm long and 4.1 mm wide, intercalated between C and E lobes along anterior border of rosette plate. E lobe subrectangular, 14.7 mm long and 8.6 mm wide, with three large low tubercles on or near anterior. E₂ lobe 14.4 mm long

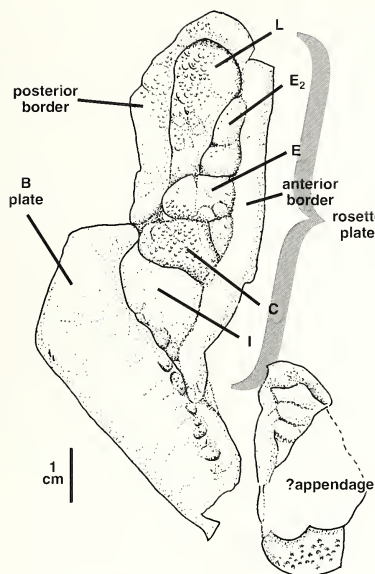


Figure 4. Sketch identifying parts of *Arthropleura cristata* Richardson, CaMNH 33853. Lettering of the rosette plate and other terminology follows that of Rolfe (1969).

and 6.8 mm wide at widest point, tuberculate, divided into two subequal parts by horizontal sulcus. L lobe irregularly and narrowly triangular, widening distally, 27.1 mm long and 13.3 mm wide; most of lobe covered by fine tubercles, proximal end also has several large low tubercles.

Another, partially preserved (?) limb (bottom right of Figures 3A&B, 4; right side of 5), elongate, with exterior surface of one end composed primarily of three parallel lobes flanked by rounded borders on two sides. Internal end of opposite side concave, with rounded, distal border and proximal border consisting of two lunate invaginations joining at midpoint, interior of this integument punctate. Exposed area of reverse side smooth. Triangular area, 24.8 mm long and 9.7 mm wide at base, preserved as mold on counterpart of fossil adjacent to lobate region (right side of Figure 5).

Discussion

The ventral side of the B plate is illustrated in Figures 3 and 4. The more-or-less straight, rounded posterior edge of the plate curves around the end of the fossil onto

the other side of the rock slab where it terminates as a straight rim. The partially preserved (?) limb (bottom right of Figures 3A&B, 4; right side of Figure 5) with its adjacent triangular integument is difficult to interpret because of its fragmentary nature. Although it is preserved near the proximal side of the B plate, this (?) limb does not appear to be attached to the B plate. The concave, punctate region of the (?) limb may be an interior view of a part of a spinous or tuberculate leg segment. The triangular integument (right side of Figure 5) may represent an adjacent part of the ventral integument of the animal. The occurrence of the (?) limb near the proximal side of the B plate, and its enigmatic shape, argue against its being part of the same leg as the B plate and attached rosette organ.

Species of *Arthropleura* are distinguished primarily by the shape, spinosity, and tuberculation of the tergites (see, for instance, Waterlot, 1934, p. 105; and Richardson, 1959). Although both tergal and limb material have been recovered from the Mazon Creek deposits, the material is not articulated.

The rosette plate of this specimen is very close in size, overall configuration, and pattern of tuberculation to a very large left rosette plate in the collections of the Field Museum of Natural History, PE 9304 (Rolfe and Ingham, 1967, plate 1, fig. 7; Rolfe, 1969, fig. 391C) that Richardson referred to *Arthropleura cristata*. For instance, in both specimens the C lobe, the L lobe, and the part of the posterior border adjacent to the L lobe, are covered with fine tubercles. A similar pattern, likely based on Mazon Creek specimens, has been depicted by Rolfe (1969, fig. 390). There are differences between the two specimens, however, the most notable being the smaller E lobe of the Ohio specimen. Also, the L lobe of the Ohio specimen is larger and less deeply dissected than that of PE 9304. The differences between the Ohio specimen and PE 9304 are of lesser magnitude, however, than the differences between PE 9304 and smaller individuals from Mazon Creek, for instance PE 154 (Richardson, 1956, fig. 40a&b; Rolfe, 1969, fig. 391B) and PE 153 (Richardson, 1956, fig. 40c&d).

The tuberculation of the lobes of the rosette plate and of the B plate of this specimen, while very close to that of PE 153, is reduced compared to that of USNM 439582 (Richardson, 1956, fig. 39), which represents a smaller, but still large, *Arthropleura* from Mazon Creek. This is contrary to the general trend of increasing tuberculation with size observed by Rolfe (1969, p. R613), but this can be ascribed to intraspecific variation.

Thus, the Ohio specimen is well within the range of variation of material found at Mazon Creek. It is certainly conspecific with specimens consisting of rosette plates, including PE 9304, that Richardson (1959) referred to *A. cristata*. It is possible that the species *A. cristata* is con-

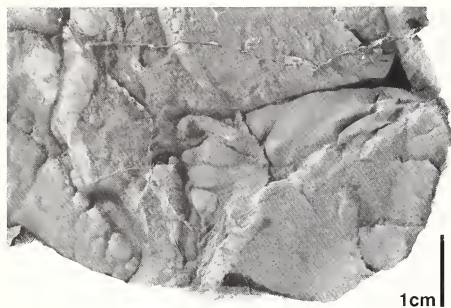


Figure 5. *Arthropleura cristata* Richardson, latex cast of part of CaMNH 33853. Whitenet. Left side of photograph shows proximal part of B plate with row of large but subtle tubercles. Middle and right of photograph shows smaller (?) limb (appendage) fragment (also seen in bottom right hand corner of Figures 3A&B) and attached triangular portion of what was originally integument (not seen in Figure 3).

specific with *Arthropleura springhillensis* (Copeland, 1957). The ornamentation on the dorsal surface of the tergites of the small species *A. springhillensis* (Copeland, 1957), which is based on several partial tergites, closely resembles that of *A. cristata*.

The pattern of tuberculation of the paratergal lobes of *A. cristata* from Mazon Creek is also similar in some ways, especially in the distribution of large and small tubercles, to that of *A. armata* Jordan. Also, the pattern of tuberculation of the paratergal lobes of *A. armata* has also recently been suggested to be variable and not as important as previously assumed for taxonomy (Hahn et al., 1986). This suggests that a reanalysis of described species of the genus is in order. The mode of preservation of the Ohio material, as a black film on a medium dark gray matrix along with carbonized plant material, is also similar to that of type material of *A. armata* housed in the collections of the Museum für Naturkunde, Berlin. This suggests similar habitats and modes of burial for the Ohio and German material.

Because a detailed analysis of Canadian and European material is beyond the scope of this paper, existing usage of the species *A. cristata* is retained here.

Size of the Arthropleura

Size of the arthropleurid from which this specimen is derived can be calculated by various means. Scaling problems are inherent with any such determination, however,

and one must expect that there would be interspecific, intraspecific, and ontogenetic variations in proportions of limb sizes versus total body length. Also, the limbs of arthropleurids have been shown to vary greatly based on position (Briggs and Almond, 1994).

The length of the anterior border of the rosette plate of the Ohio specimen, measured from the intersection of its posterior margin with the B plate to the most distal point of the anterior border opposite that intersection point, is 65 mm. The length of the anterior border of a well-preserved Mazon Creek specimen (USNM 439582) is about 36 mm. The entire leg complex of the USNM specimen is about 127 mm. Assuming similar proportions, the Ohio leg would have been 229 mm long. Such a leg would belong to an animal whose tergites would be a minimum of 458 mm wide, that is, the length of two legs. Consideration of the sternal plates would add width, as the legs would be separated by sternites. However, if the legs projected from the tergites, as seen in some reconstructions (e.g., Rolfe, 1969, fig. 387; Hahn et al., 1986), the additional width added would be reduced. The legs do not project from beneath the tergites in the reconstruction of Almond and Briggs (1994, fig. 2). That reconstruction, however, is based upon juveniles which were much smaller than the specimens studied here. Using the proportions of the reconstruction of Rolfe and Ingham (1967; fig. 387 in Rolfe, 1969) the length of a specimen with a width of 458 mm would slightly exceed 1.5 m. The estimated length of the specimen would be longer (greater than 2 m) using the length-to-width ratio of the more elongate reconstruction of Hahn et al. (1986, Abb. 2). Also, the number of segment numbers borne by adults of the genus are not known with certainty. Hahn et al. (1986) estimated a minimum number of 30 body somites for *Arthropleura armata* Jordan, but this and other species may have had additional segments. Thus, the true length of the specimen described here may have been even longer.

ARTHROPLEURA cf. *A. CRISTATA*

Figure 6

Material studied

YPM-PU 88076, formerly at Princeton University, now in the Yale Peabody Museum's Entomology collection. The specimen consists of a partial left rosette plate, an attached partial B plate, a disarticulated K plate, and an elongate, disarticulated fragment that may or may not belong to the specimen. The specimen was preserved on two counterparts, one of which (marked with an old no., M. 855) was examined as part of this study. A latex mold of the Yale specimen made by Donald Baird, FMNH PE 26148 (Figure 6), was also examined as part of this study. According to the Yale and Field Museum labels, the specimen was collected by I. F. Mansfield in 1877 from his mine at Cannellton, Darlington Township, Beaver County, western Pennsylvania. The specimen is preserved in a

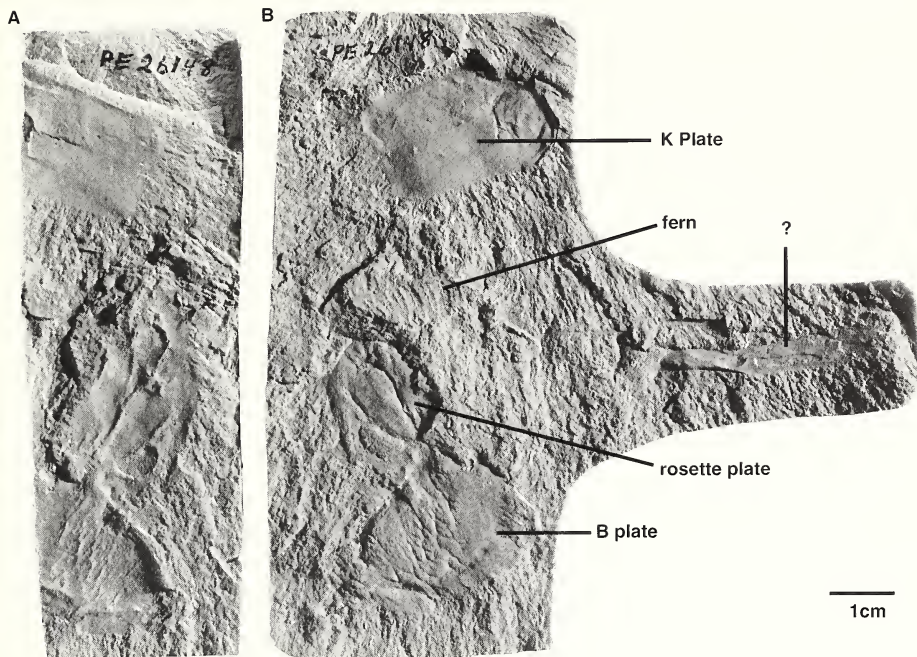


Figure 6. *Arthropleura* cf. *A. cristata*. FMNH PE 26148 (a latex cast of YPM-PU 88076), from Cannelton, western Pennsylvania. Collected by I. F. Mansfield. Molds of part (A) and counterpart (B). Specimen includes a partial rosette plate, an attached partial B plate, a disarticulated K plate, and an elongate, disarticulated fragment (indicated by a "?") that may or may not be related to the specimen. A fern is also present.

grayish black shale ("cannel slate") found below an Upper Kittanning canal coal within the Kittanning Formation, Allegheny Group, Middle Pennsylvanian (approximately middle Westphalian D, Baird, 1978, p. 14; or Desmoinesian in Midcontinent terms).

Fragments of plant material, including a fern fossil, are preserved on the slab containing the arthropleurid. The fern is located between the K plate and the rosette plate/B plate, just below the level of the arthropleurid material. The Cannelton locality has yielded a number of plants, eurypterids, insects, and fish. Additional information on this locality and its fauna can be found in Baird (1978).

Description

Left B plate and closely associated rosette plate (bottom of Figures 6A&B), and separated K plate (top of

Figures 6A&B), large for genus. B plate subrectangular, preserved section about 30 mm long and 23 mm wide, midsection coarsely covered with large but subtle tubercles; thin groove, approximately 4 mm from edge, runs along posterior. Rosette plate with prominent anterior border and several preserved lobes. (?)C lobe subovate, 7.7 mm long (maximum length) and 3.9 mm wide, covered with fine tubercles. (?)E lobe subtriangular, 14 mm long and 7 mm wide (maximum width), with acutely pointed posterior corner. Small, 2.9 mm x 8 mm, triangular lobe intercalated between presumed C and E lobes and anterior border. Other lobe(s) of rosette plate indistinct. K plate subrectangular, mostly smooth, with rounded rims; rims on the (?)distal side more strongly rounded. Maximum width 30 mm, 17.6 mm long at midpoint. Proximal edge straight; distal edge curved. Two subcentrally located par-

allel longitudinal ridges join Y-shaped ridge near distal side (Figures 6A&B).

Discussion

The rosette and B plates of this specimen are incomplete, making interpretations of specific features difficult. It is difficult to be sure that the lobe identifications are correct. The ridges on the K plate may be taphonomic.

An elongate object (labeled "7" on Figure 6), 37 mm long and 5.4 mm wide, with longitudinal wrinkling, is associated with the specimen. Its mode of preservation as a black film is similar to that of the certain arthropleurid material. It is possible that this elongate object may represent a part of the arthropleurid, for instance the edge of a tergite.

The Pennsylvania specimen is smaller than the Ohio specimen. Except for the greater rugosity of its B plate, the Pennsylvania specimen is of about the same overall rugosity. That greater rugosity of the B plate, however, is less than that of the B plate of USNM 439582, a specimen from Mazon Creek. The Pennsylvania material is flattened more than the Ohio material and is preserved in a darker shale. But, like the Ohio material, it is preserved as a thin black film. The Pennsylvania specimen may be conspecific with the Ohio and Illinois material, but final determination awaits additional material.

Based on USNM 439582, the length of the K plate of *Arthropleura cristata* is subequal to the length of the rosette plate. If the Pennsylvania specimen is conspecific, the reconstructed length of that specimen would then be about half the size of the specimen from Ohio; that is, the minimum length of the reconstructed animal would be a little less than 0.75 m. Proportions based on the C lobe of the Ohio specimen and the questionable C lobe of the Pennsylvania specimen would give a roughly similar figure, giving credence to this minimum length. Using measurements of the K plate of other species of *Arthropleura* give different figures. The K plate of a specimen of *Arthropleura manniata* (Salter) from the Netherlands that was described and illustrated by Hahn et al. (1986, Abb. 3) has reconstructed dimensions of 60 by 40 mm, representing, according to Hahn et al., an animal with a total length of ≥ 2 m. The K plate of the Pennsylvania specimen has dimensions roughly $\frac{1}{2}$ of those of that specimen from the Netherlands. Using these proportions the minimum length of the Pennsylvania specimen would be somewhat longer than 1 m.

Conclusions

The specimens described here extend the geographic and stratigraphic range of *Arthropleura* in North America. The geographic range of the species *A. cristata* is extensive; the Mazon Creek site is 650 km from the 7-11 site. The stratigraphic range of body fossils of *Arthropleura*

found in North America extends from the Atokan into what is probably the lower Missourian. This stratigraphic range is well within that reported for European occurrences of body fossils of *Arthropleura*.

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Work on this paper would not have been possible without the kindness extended by Mr. Gregory A. McComas of Marion, Ohio, who not only discovered the Ohio specimen and donated it to the Carnegie Museum of Natural History, but also provided information on the 7-11 site and its stratigraphy. Donald Baird, Pittsburgh, Pennsylvania, called attention to the specimen from Pennsylvania, which had been originally identified as *Arthropleura* by W. D. Ian Rolfe. Dr. Baird also provided information on the Pennsylvania locality and the Linton site. Jann Thompson, U.S. National Museum of Natural History; Gregory Buckley, Field Museum of Natural History; John Carter and Albert Kolar, Carnegie Museum of Natural History; and Erika Pietrzeniuk, Museum für Naturkunde, loaned specimens and/or facilitated visits to their respective institutions. Russell White, Yale Peabody Museum (YPM), located the original specimen from Pennsylvania, which was loaned by Raymond Pupedis (YPM). Photographs were taken by Bruce Frumker, The Cleveland Museum of Natural History (CMNH). David Condon and Suellen Hopfer (CMNH) provided translations, and Shya Chitaley (CMNH) identified plant material. This paper was improved by critiques or reviews by Derek Briggs, University of Bristol; William Shear, Hampton-Sydney College; Paul Selden, University of Manchester; R. M. Feldmann, Kent State University; and W. D. I. Rolfe, Edinburgh.

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FOSSIL YAK (*BOS GRUNNIENS*: ARTIODACTYLA, MAMMALIA) FROM THE HIMALAYAS OF PAKISTAN

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ABSTRACT

We describe a maxilla with DP2/-M1/ and associated edentulous mandible for a Quaternary yak (*Bos grunniens* Linnaeus; Bovidae) from Skardu Basin (Northern Areas, Pakistan). The specimen was found in a short stratigraphic section that may represent an alluvial fan. Fossils from high altitudes are rare, and the fossil record for mountain animals is poor. This specimen is the first fossil vertebrate from the Pakistani Himalayas, and one of a few yak fossils known.

Introduction

Skardu Basin is in the Northern Areas of Pakistan on the confluence of the Shigar and Indus rivers. It is approximately 75 km east of Nanga Parbat (the eighth highest mountain in the world) and 80 km southwest of K-2 (the second highest mountain in the world) and forms part of the boundary between the high Himalayas and the Karakorum Mountains (Searle, 1991). Although immediately surrounded by peaks of around 4900 m, base elevation is only around 2200 m (Cronin, 1989). Active uplift continues in this part of the Himalayas, and the basin has been a high altitude environment for all of the late Cenozoic. In spite of this, its geomorphological history is diverse. In the Pliocene and early Pleistocene, glacial deposits, periglacial lakes, and alluvial fan conglomerates were deposited (Bunthang Sequence, Cronin et al., 1989). During the last glaciation, the entire basin was covered by a glacial lake when the Indus was dammed by a moraine (Skardu Lake Beds, Cronin, 1989), possibly as late as 30,000 years ago (Schroder et al., 1989).

In May and June of 1994, we undertook a survey expedition to Skardu Basin and its surrounding areas to assess its potential to yield vertebrate fossils. Our intention was to find sediments that might match the fossiliferous Eocene-Oligocene sediments of Ladakh, 100 km southeast of Skardu (Savage et al., 1977; Nanda and Sahni, 1990). Rocks of this age appear to be exposed on the road from Skardu to Khamang (Khan et al., 1988), but our inspection suggests that they are too heavily metamorphosed to yield fossil vertebrates. Therefore, we redirected our attention to the sediments of Skardu Basin. No fossils have been reported from the sediments of the basin, and these rocks would offer a unique opportunity to sample a late Cenozoic high-altitude fauna.

Material

The recovered fossils are part of the Howard University-Geological Survey of Pakistan collections (H-GSP) and will be permanently housed at the Stratigraphy and Paleontology Branch of the Geological Survey of Pakistan in Islamabad.

We used the following collections of extant mammals for comparisons: CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; UCMP, University of California, Museum of Paleontology, Berkeley, California; USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C.

Localities

We recovered two fossils, both within sediments at the southeast facing slope of the Marshakala Massif. A terrace of approximately 1 km width extends from the foot of this mountain to the Indus (in the east). This terrace is deeply cut by numerous gulleys with steep bare slopes on the east side of the road. This is Howard-Geological

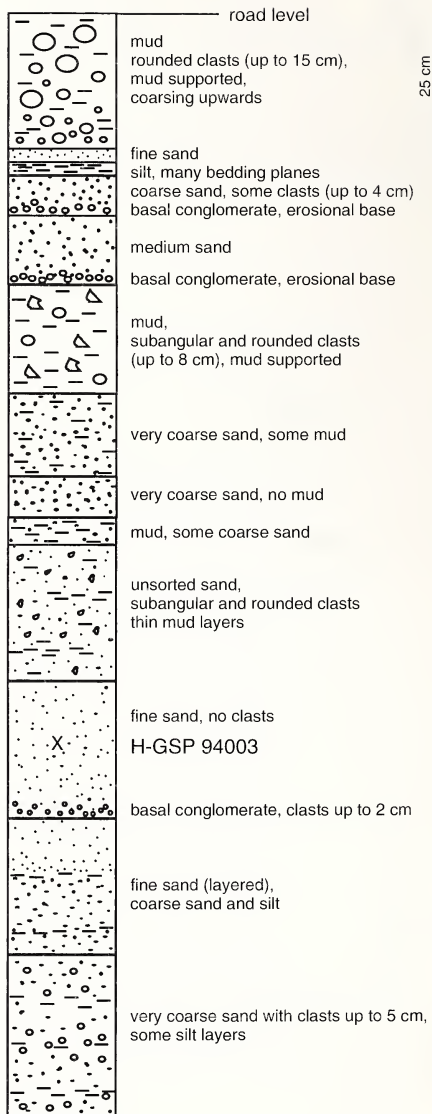


Figure 1. Stratigraphic section of H-GSP Locality 9403 near the foot of the Marshakala Ridge in Skardu Basin. Position of fossil yak (H-GSP 94003) is also marked.

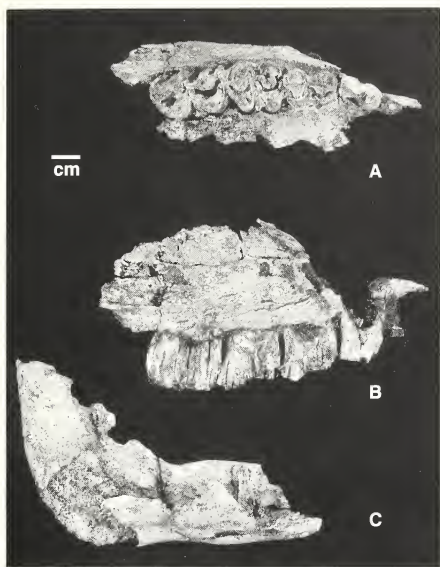


Figure 2. *Bos grunniens*. Fossil yak (H-GSP 94003) from Skardu Basin, unretouched photographs of occlusal (A) and lateral (B) views of right maxilla and associated right mandible in lateral view (C).

Survey of Pakistan (H-GSP) Locality 9403; its coordinates are approximately 35°20'N, 75°41'E. This locality yielded the yak specimen described here (H-GSP 94003). It was found in a north-facing slope in one of the northernmost gulleys near the road. Figure 1 shows a profile taken at the site of the fossil.

Searle (1991, fig. 11.4) mapped the area of this locality as alluvial fan sediments, which suggests that the specimen is of Holocene age. This is the most likely interpretation of the limited amount of geological data available (Schroder, personal communication). Alternatively, it is possible that the bottom of the section of Figure 1 crops out in the Skardu Lake Beds. These deposits form a plain in the basin approximately 30 m above the present Indus (Cronin, 1989) and this would include the elevation of Locality 9403. This would imply that H-GSP 94003 is late Pleistocene in age.

A second fossil was recovered on the west side of the road. Here exposure is mainly along one long escarpment facing northeast and extending from the foot of Marshakala to the road and beyond. This locality (H-GSP Locality 9401) yielded a fragment of a lumbar vertebra (H-GSP

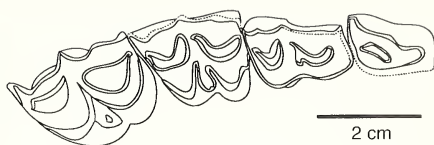


Figure 3. *Bos grunniens*. Fossil yak (H-GSP 94003) from Skardu Basin, outline drawing of right maxillary dentition.

94001) of a bovid, from beds corresponding to the top layers of the profile of Figure 1. It is certainly part of the alluvial fan of Marshakala.

Systematic Palaeontology

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1828

Subfamily BOVINAE Gray, 1821

Genus *Bos* Linnaeus, 1758

Bos GRUNNIENS Linnaeus, 1766

Figures 2-3

Description

The mandible (Figure 2) is edentulous, preserving the base of the left ramus and proximal portion of the corpus. The alveolus for the first molar is approximately 27 mm in length and 11.5 mm in width. There is no indication that the second molar is developing within the corpus. The ramus is broken, exposing a broad groove for the mandibular canal that passes immediately caudal to and then directly inferior to the first molar alveolus to lie at the base of the corpus. The preserved base of the ramus is transversely narrow and forms a slightly obtuse angle with the corpus, in a manner similar to the juvenile *Bos grunniens* examined (UCMP 55145).

The maxilla (Figure 2) preserves the alveolar portion which houses DP2-4/, and the first permanent molar. The lateral face of the maxilla bears a low roughened facial tuber, lying roughly 15 mm above the alveolar margin between the DP3/ and DP4/. Erosion of the lateral wall of the maxilla near the maxillary-zygomatic margin exposes a canal (5 mm wide) that extends rostrally. It probably contained the caudal alveolar branch of the trigeminal nerve that travels toward the molar row (Getty, 1975). The palatine process of the maxilla is thick caudally, but tapers to a thin plate rostrally, lingual to the premolars.

It is likely that the thick plate of alveolar bone at the posterior surface of M1/ forms a socket for an erupting M2/, although there is no wear at the caudal margin of M1/ that would imply contact between M1/ and M2/. The first molar is unworn. The tooth is 24.8 mm long and 14.4 mm wide at

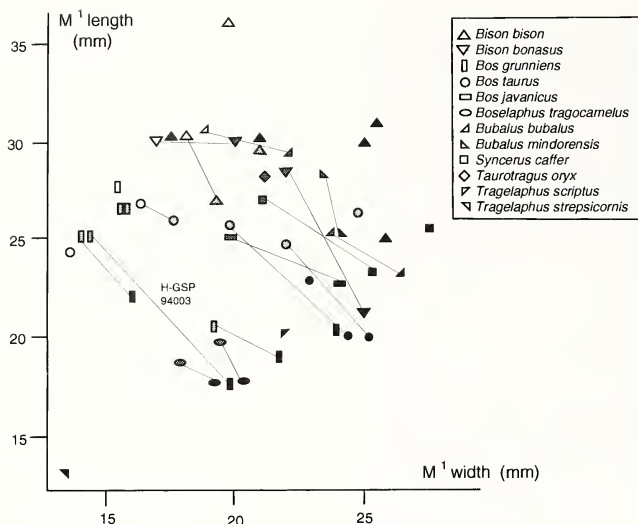


Figure 4. Bivariate plot for length and width of dental measures of M1's of Bovini. Included are three species of *Bos*, two species of *Bison*, two species of *Bubalus*, two species of *Tragelaphus*, *Syncerus caffer*, *Boselaphus tragocamelus*, and *Taurotragus oryx*. Unfilled symbols identify occlusal measurements of unworn teeth. Solid symbols identify measurements at the enamel-dentin junction (either measured on extremely worn or broken specimens). Symbols for the same specimen are connected by a line that summarizes shape change of the tooth as a result of wear during its life. Gray figures represent occlusal measurements of worn teeth at the time of death of the animal (i.e. measurements of the occlusal surface of museum specimens). Gray symbols thus represent points on the trajectory connecting unfilled and solid symbols.

its occlusal surface, and 17.5 by 19.8 mm at its base, which is visible on the broken medial side of the specimen. The enamel-dentin junction (EDJ) has not developed, and overall molar shape indicates that the occlusal shape decreases in relative length and increases in relative width during development. This trend was observed to varying degrees in all of the bovids examined (see discussion).

The dentition displays the typical bovid selenodont form (Figure 3). The entostyle (median basal pillar of Gentry, 1970, p. 544) of M1/ is robust, and does not reach the occlusal surface. The labial styles flanking the metacone are more strongly developed than the parastyle, although the latter cusp is larger than the metacone. DP4/ also bears a well developed entostyle, and is both shorter (17.0 mm) and narrower (17.5 mm) than the first molar as measured at the EDJ. All four cusps are equally well developed. In DP3/, both the proto- and paracone are reduced bucco-lingually, while the hypo- and metacone are wider than the anterior cusps, making the rostral half of the premolar longer and narrower than the caudal half. Overall, the maximum length and width of DP3/ are 17.9 mm and 15.3 mm. Only the metastyle of the

DP3/ is well developed. DP2/ bears a small paracone, a metacone, and its protocone is larger than in DP3/. It does not have a hypocone, and only the metastyle is strong. The tooth is narrow and long, its length is 16.2 mm, its width 11.5 mm.

Discussion

Bovids form a distinct, diverse, and important family, but their classification at levels below the family remains in dispute. We follow the subfamily classification of Wilson and Reeder (1993). The most diagnostic osteological characteristics of the members of the Bovidae are in the horncores (Pilgrim, 1937; Koenigswald, 1986), although dental characteristics can be of limited usefulness (Gentry, 1970). Large size and presence of a large entostyle suggest that H-GSP 94003 pertains to the subfamily of cattle: Bovinae. Wilson and Reeder (1993) included the extant genera *Bison*, *Bos*, *Boselaphus*, *Bubalus*, *Syncerus*, *Taurotragus*, *Tetracerus*, and *Tragelaphus* in Bovinae. Of these, extant and fossil forms of *Syncerus*, *Taurotragus* and *Tragelaphus* are restricted to Africa and Arabia (Gentry, 1970), and it is unlikely that H-GSP 94003 pertains to these.

The fossil record of Bovinae in Indo-Pakistan is extensive (Pilgrim, 1937; Simpson, 1945), but most of these bovids are restricted to the lowlands and are thus unlikely to be found in the Skardu Basin. Among these are *Tetracerus*, which is also small and lacks an entostyle, and *Boselaphus*, which matches H-GSP 94003 in size but either lacks entirely or retains a very small entostyle (USNM 144075, 269127). The remaining extant genera, *Bison*, *Bos*, and *Bubalus*, and their Pleistocene relatives, such as *Leptobos* and *Hemibos*, are essentially indistinguishable on the basis of tooth shape. The modern species of *Bos* and *Bubalus* that occur on the Asian mainland do not live in high altitude environments (Nowak, 1991), with the exception of the yak, *Bos grunniens*. Fossil large bovids are also only known from lowland environments, although the fossil record from high altitudes is so scarce that this cannot be taken as evidence for their absence.

Olsen (1990) reviewed the fossil record for yaks and discussed some of their morphological differences with other bovids. His figures of dentitions show great differences in the occlusal morphology between the modern genera of large Bovinae. These differences, such as the squareness of teeth, are due to individual age of the animals as suggested by Olsen. The yak that is figured was a dentally aged animal, with an M1/ that had nearly lost its internal enamel folds. The *Bos taurus* specimen that Olsen (1990) figured lost its P2/ after death (given that its alveolus is visible), and his *Bubalus* is a young individual that retains a DP4/ with four cusps (instead of a P4/ with only two).

The fossil record for yaks is poor: few Pleistocene specimens are known from high elevations of Central Asia (Olsen, 1990). There is no consensus on how to distinguish (dental) remains of *Bison*, *Bos*, and other large bovids from late Cenozoic of Asia, leaving the evolutionary history of the yak uncertain. This is significant because molecular evidence suggests that the sister group of *Bos grunniens* is *Bison bison*, not *Bos taurus* (Miyamoto et al., 1989).

Size can be used to distinguish between the extant species of Bovinae to some extent. Figure 4 shows M1/ size distribution for several Bovinae. For each specimen, length and width were measured at the occlusal surface and at the enamel-dentin junction (when it was visible). Because bovid molar dimensions change with wear, there are only two wear stages that are independent of age and at which animals can be compared directly: at the occlusal surface of unworn teeth (unfilled symbols) and at the enamel-dentin junction (solid symbols). Occlusal "ontogeny" results from wear and open and closed figures represent its extremes. These extremes are connected by an ontogenetic wear trajectory, indicated diagrammatically as straight lines in Figure 4. In teeth that have been in use, the unworn dimensions cannot be determined and we therefore measured these teeth at the occlusal surface. If the lines represent the true ontogenetic trajectory, then the dimensions of the

occlusal surface of a worn tooth (gray symbols) will be on this line. They represent the wear stage at the time of death.

While size comparisons cannot be used as the sole identifier among bovine teeth, comparing the occlusal ontogenies of different bovids suggests that the most likely identification of H-GSP 94003 is *Bos grunniens*. It is close in its overall dimensions to the six yak specimens that we measured (UCMP 55145, USNM 14328, USNM 257034, USNM 270919, USNM 296176, USNM 396176). Its final wear stages are similar in size to *Boselaphus*, but this genus differs morphologically in having a small or absent entostyle. The only other bovid that comes close in size to H-GSP 94003 is a domestic dwarf bull (*Bos taurus*, USNM 17971, open circle near y-axis). It is unlikely that the fossil represents a dwarf bull, but the specimen does show the size plasticity among bovids.

Not only do the M1/ dimensions of H-GSP 94003 match those of modern yaks, the deciduous premolars are also similar in size to the only deciduous yak premolars we could measure. In UCMP 55145 DP2/ was 16.2 by 9.3 mm, DP3/ was 19.1 by 13.2 mm, and DP4/ was 19.0 by 16.2 mm.

The evidence for identification of H-GSP 94003 is circumstantial but firm. Morphological traits, the size of entostyle and labial styles identify the specimen as pertaining to *Bison*, *Bos*, *Bubalus*, *Syncerus*, or their immediate fossil relatives. The habitat in which the animal must have lived suggests strongly that it was a yak, and the size data on the teeth confirm this identification.

Acknowledgments

The Geological Survey of Pakistan provided logistic support in the field and orchestrated the administrative aspects of our work in this politically sensitive region. We drew extensively on the geological and geomorphological knowledge that Dr. J. F. Schroder (University of Nebraska at Omaha) provided for our field area. Drs. John Barry (Harvard University) and Paul Koch (Princeton University) reviewed the manuscript. The curators of the CMNH, USNM, and UCMP mammal collections provided access to comparative material. Field work was financially supported by a grant from the L. S. B. Leakey Foundation to J. G. M. Thewissen. We thank all for their help.

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KIRTLANDIA[®]

The Cleveland Museum of Natural History

March 1997

Number 50: 17-20

PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

PRESENTATION OF THE AWARD

MIRIAM SMEAD

Trustee, The Cleveland Museum of Natural History

1 Wade Oval Drive, University Circle

Cleveland, Ohio 44106 -1767

Tonight we have gathered to pay tribute to Dr. Edward O. Wilson, the recipient of The Cleveland Museum of Natural History's David S. Ingalls, Jr. Award for Excellence. Just who is this man and why has he gained international prominence?

Dr. Wilson was born in Birmingham, Alabama. An only child in a family that moved frequently, Edward attended fourteen different public schools in eleven years. In his nomadic life, Nature became his most reliable companion. It was his delight to explore the woods and swamps along the Gulf Coast. Of this he later wrote, "The outdoors was the one part of my world I perceived to hold rock steady." Fortunately for the world of biology, his interest focused on insects. It was at the age of sixteen that his fascination for ants developed. He was determined to survey all of the ants in Alabama! As a dedicated student of nature, he was active in scouting and achieved Eagle Scout rank by the age of fifteen. Years later, his enthusiasm for scouting led him to include the Boy Scout Oath in *Naturalist* (1994), his autobiography.

Dr. Wilson graduated Phi Beta Kappa from the University of Alabama, and received his doctorate in biology from Harvard University. In addition to entomology,

he also studied population biology, ecology, and biogeography. Today he is Pellegrino University Professor, and Curator in Entomology at the Museum of Comparative Zoology, at Harvard University. His literary productivity is awesome. With extraordinary drive, he has produced nearly 350 scientific papers and at least twenty books. The stimulus to scientific thought caused by his book *Sociobiology: the New Synthesis* (1975), earned him the title "father of sociobiology." His application of that discipline to humans led to his Pulitzer Prize winning book, *On Human Nature* (1978), a fascinating view of the basis in biology for human behavior.

In 1986, he helped to convene leading researchers, naturalists, and conservationists to explore the nature of biodiversity, bringing this term into widespread popular usage. His book, *The Diversity of Life* (1992), became the "bible of the biosphere." One critic wrote, "It is written with a lucidness that borders on poetry." This book helped to focus public concern on the catastrophic loss of global biodiversity and the importance of conservation. With the late Robert MacArthur, Dr. Wilson formulated the theory of island biogeography, a theory which has had a tremendous impact on conservation practices.

*On May 9, 1995, the David S. Ingalls, Jr. Award for Excellence was presented to Edward O. Wilson. A slightly shortened version of Miriam Smead's speech on that occasion is printed here. Edward O. Wilson's remarks are excerpted from his acceptance speech.

Dr. Wilson is one of the world's most respected authorities on ants. Of this subject he has written copiously. His book *The Ants* (1990), written with Bert Hölldobler, won a Pulitzer prize.

He has been an active conservationist. With deep concern he promotes the conservation of endangered species. Dr. Wilson cautions, "The loss of species is the folly our descendants are least likely to forgive us." A compelling advocate for his beliefs, it is not enough for Dr. Wilson to merely write of these important concerns. He is a trustee of The Nature Conservancy and the American Museum of Natural History, and has chaired the National Research Council's Committee on Biodiversity. Because of his dedication to conservation, Dr. Wilson encourages young people to pursue careers as advocates for the environment. In honor of this commitment, there will be an E. O. Wilson summer intern in our Kirtlandia Society Adopt-A-Student program in 1996. It will be funded by the Museum's Natural Areas Endowment.

This distinguished international scholar, whom we honor tonight, is the quintessential field biologist in an age when much of academia has turned to molecular biology. Through his keen observations, astute evaluations, clarity of writing, and forcefulness of teaching, this scholar has led the contemporary scientific world, and those of us less scholarly, to a greater understanding of ourselves and of the evolutionary process.



Dr. Edward O. Wilson. Photograph by Jon Chase, Harvard News Office.

REPLY

EDWARD O. WILSON

*Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138-2902*

Mrs. Smead, Dr. Taylor, Mrs. Ingalls, Mary Lou Ferbert, other members of the Linnaean Society, members of the Museum staff, and students — I am overwhelmed. Thank you so much for this wonderful tribute. I am tempted to give a response that Salvador Dali gave. It was history's shortest speech. He said "I'll be so brief, I have already finished," and he sat down. But if you will be indulgent, I thought I might make a few remarks in minute recompense for the extraordinary honor of the Ingalls award and this warm reception that I have received here in Cleveland.

I want to say a few things about biodiversity, because it is to organizations like this one that we must look now increasingly for education, for research, and for progress in preserving this most important and irreplaceable part of the world heritage in order to pass it on to future generations.

We are in a period of slight environmental backlash in Washington, and in the beginning of what I call the backlash environmental literature, telling us that things aren't quite as bad as some of the environmentalists have been claiming, and pointing to the fact that there has been real progress in the United States in cleaning the air and restoring rivers and lakes. But, lest we become over-confident because of this local progress in the United States, I would remind you of the devastation of Eastern Europe and the Soviet Union and of the fact that the tropical countries of the world, where two-thirds of the people of the world live, and where far more than half of all the species of plants and animals live, is in severe decline in every respect. I think that very few of the anti-environmentalist critics will deny that fact. It does little to concentrate and to rest on limited success stories in this country. The devastation that is continuing to occur around the world with the exponential growth of human beings and the rising expectation of people everywhere in the world for higher energy and materials consumption has resulted in habitat destruction, and that in turn translates into mass extinction of species and races.

Roughly one hundred thousand species are known to be native to the United States. Some 1.5% of those species in the best known groups, such as birds, amphibians, and flowering plants, have become extinct. About 22% according to the data base of the Nature Conservancy, are endangered, threatened or rare.

Ten years ago I estimated that worldwide about 1.4 million species have been described and given a scientific name. Other estimates since that time have raised the number of species known to science to be about somewhere between 1.5 and 1.8 million. The important point here is that nobody knows exactly how many species have been given a scientific name. And we certainly don't know how many species there are in the world, because so little has been done of research of the kind at which The Cleveland Museum of Natural History excels. This museum represents one of a very small number of institutions capable of doing this kind of research and making the results known to the public as part of a sustained, educational enterprise. Let me add my appreciation of the Natural Areas program of the Museum, something that has been conducted in concert with efforts of the Nature Conservancy and which is devoted to identifying, helping to set aside, and then studying on a long-term basis the remaining natural areas of Ohio.

The most exciting things immediately ahead of us is to explore this planet. Every group of organisms is still open to exploration. If you want to discover new species, all you have to do is pay attention to organisms that are a fraction of an inch, say several millimeters long or less, and start studying them. In every section of this microscopic and submicroscopic world can be found different ecological niches allowing small insects, roundworms, protozoans, bacteria, and other tiny creatures to divide up the diversity so that they can live in a single square meter area by the thousands of species. A rotting stump in a forest seems an inconsequential object to us, but in fact to creatures as small as insects or smaller it can be the equivalent of an island like Puerto Rico. One can find organisms by the tens to hundreds of thousands, representing hundreds of species, in a place like this. A large percentage of them are outright unknown to science, that is, not even having a scientific name (that would be a small minority in most cases in Ohio). Wherever you go in the world, a vast majority of them are unstudied—we don't know what their life cycles are, what their biology is or anything.

They include oribatid mites. These small creatures look like a cross between a turtle and a spider. They spend their lives apparently feeding on—no one knows for sure—fungal spores and rotting debris. They are clearly a

major part of the ecosystem. About five years ago I undertook a study of very small ants that live in leaf litter around the world. There are hundreds of species of these tiny ants whose biology is completely unknown. I guessed that they might be feeding on mites because these creatures were present there in millions. The ants are not much larger than they are. We might have miniature lions and tigers and wolf packs represented by the ants, hunting through the litter and collecting these mites like antelopes and rabbits. Who knows? We didn't know; we didn't have any information. So I began the study and I soon discovered that this was indeed the case. There were ants that do hunt oribatid mites in particular. They pick them up like watermelons and cantaloupes out of the litter and they take them back to the nest and then pop them open and they feast on them. And that's how they make their living, at least in part, and the activity is clearly an important part of the energy cycle of the forest.

So, in order to find out about oribatid mites I looked around for an expert. I thought that surely there was all kind of expertise available to help me identify these mites and tell me about them. Quite the contrary: I found there is only one specialist in the entire United States working on oribatid mites full-time; that's Roy Norton at the University of Syracuse. Fortunately he is a very coopera-

tive scientist, and so we exchanged a lot of information. He was fascinated to know about the ants who feed on them. He said, "We know almost nothing about the predators." And I said, "Good, we know almost nothing about the food these ants eat." But we didn't get very far with this because there were only two of us, and we both had other things to do. I just give you this as an example of what needs to be done in ecology and systematics.

As part of the effort of biodiversity studies we have the extremely practical issue of finding out where the endangered species of plants and animals are. We need to get moving on this type of research, because this is the kind of information that will not only produce new scientific knowledge, but also provide the basis for future conservation programs. It will help guide future environmental legislation. It will also serve as the foundation of rational regional planning. We need increasingly to seek solutions satisfactory for both conservationists, whose precept is to save as much biodiversity as possible, and landowners and business, who must get on with managing their private property and in some cases developing it. Societies can arrive at such win-win strategies, I believe, but ultimately they will need the kind of scientific knowledge that only a few institutions, such as The Cleveland Museum of Natural History, can provide.

KIRTLANDIA[®]

The Cleveland Museum of Natural History

March 1997

Number 50:21-24

PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

PRESENTATION OF THE AWARD

MIRIAM SMEAD

*Trustee, The Cleveland Museum of Natural History
1 Wade Oval Drive, University Circle
Cleveland, Ohio 44106-1767*

Tonight we have gathered to present the fourth David S. Ingalls, Jr. Award for Excellence. It is awarded to an individual for excellence in research, education, or conservation in one of the fields of natural science represented by The Cleveland Museum of Natural History. Dr. Roger Conant, our honoree, has become a giant of national and international prominence in all three of these areas and his remarkable contributions to herpetology and the zoo community span seven decades.

Born in Mamaroneck, New York on May 6, 1909, his zoological career began in Ohio. In 1929 he was appointed to the position of Curator of Reptiles at the Toledo Zoo, from which he was promoted four years later to General Curator. Those years spent, in part, researching Ohio's herpetology resulted in the publication of his first book, *Reptiles of Ohio*, in 1938. It soon became a landmark in the field of herpetology, with its innovative spot-mapping technique that related species distributions to the habitats in which they were recorded.

In 1935 he returned to the East and accepted the position of Curator of Reptiles at the Philadelphia Zoological Garden. During his association there he wrote and presented a weekly radio program entitled, "Let's Visit the Zoo" that

began in 1936 and was aired for over 33 years. Also, under his guidance the Philadelphia Zoo was involved in some of the earliest captive breeding programs. His concern for the proper management of captive animals stimulated research and addressed critical issues of conservation. In 1967 he was appointed Director of the Philadelphia Zoo, a position which he held until his retirement in 1973.

Through his books he has attracted countless young people to the delights of studying and identifying reptiles and amphibians. In the late 1950s he prepared the Boy Scouts of America Merit Badge Pamphlet on Reptile Study. Since then over 200,000 young boys have earned that merit badge. Hundreds of thousands of others have learned more about reptiles by using that pamphlet. The strong influence of Dr. Conant's presence and research in Ohio resulted in the formation of the Ohio Herpetology Society. This later grew into the Society for the Study of Amphibians and Reptiles, now the largest herpetological society in the world.

Perhaps the publication for which he is best known is his *Field Guide to Reptiles and Amphibians of Eastern and Central North America*, in the Peterson Field Guide Series. First published in 1958, it has gone through three editions. This handbook has had a great impact in stimulating interest

*On June 1, 1996, the David S. Ingalls, Jr. Award for Excellence was presented to Roger Conant. A slightly shortened version of Miriam Smead's speech on that occasion is printed here. Roger Conant's remarks are excerpted from his acceptance speech.

and educating people in the field of herpetology. In Roger Tory Peterson's letter of endorsement for this award, he wrote, "He (Conant) has done more than anyone else to enhance our knowledge of reptiles and amphibians in the United States."

Collaborating with the late Howard K. Gloyd, former Director of the Chicago Academy of Sciences, the book *Snakes of the Agkistrodon Complex*, was published in 1990. It is a monograph on the genus *Agkistrodon*, which includes the copperhead and its relatives worldwide. Our honoree has authored over 200 scientific papers, representing research, not only in North America, but in Latin America and Asia as well. He has been the recipient of many awards and recognitions.

Spanning seven decades of research, his books have brought the world of reptiles into the homes of innumerable readers. He has been a highly respected spokesman for greater public understanding of this often misunderstood group of animals. Through faithful correspondence he has been a strong influence in the lives of budding naturalists. Countless herpetologists and naturalists today write with great admiration and genuine fondness for this man who has been their mentor and friend.

Dr. Conant, we salute you and all of the accomplishments of your 87 years. Your efforts and accomplishments embody the very principles of this Museum's mission. On behalf of the Board of Trustees of The Cleveland Museum of Natural History, I am highly honored to present you the David S. Ingalls, Jr. Award for Excellence.



Roger Conant, June 1, 1996

REPLY

ROGER CONANT

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Thank you Dr. Taylor, Mrs. Smead, and all of you for being here, and especially for this award. Accepting it is certainly one of the highlights of my career and especially in my old age, if I may put it that way. However, I am overawed by the company with which I find myself: the distinguished scholars Steven Jay Gould and Edward O. Wilson; and Roger Tory Peterson, whom I have known for over forty years. And here I am, a self-taught naturalist, among them. I feel highly honored indeed by the presentation of this award and by the recognition that goes with it.

I fancy myself as a humble interpreter of natural history and of zoo management and zoo animals, especially for young people. I have received a lot of letters from youngsters, and I have tried to answer all of them. One of them surfaced just this very evening—a letter I wrote back in 1970 to a then teenager. He cherished that letter and I am happy to see that he still has it.

I have gotten a lot of letters that read something like this: "Dear Mr. Conant, I have just found a snake that is an eighth of an inch longer than the maximum size that you give in your field guide. How do I go about putting this wonderful discovery on record?" I wrote back nice letters to them. I didn't tell them that snakes stretch and that they should be measured when they are relaxed. That would have taken all of the fun out of it for them. My extensive files and my mailing log indicate that during my lifetime I have written more than 15,000 letters, chiefly to young people, trying to answer their questions no matter how trivial. Usually I can do them off the top of my head, but I will admit there have been times when I had to do a lot of research to answer their questions. But I persevered and wrote to them anyhow.

During my tenure as Director of the Philadelphia Zoo, and in fact even before that, when I was in a subordinate position, I always found time to help budding young people. Often a teenager would arrive with one or both parents who were anxious to know whether it was possible for the young person to earn a living in herpetology. Unhappily, in those days, I had to tell them that the answer was "no." There were very few opportunities in herpetology. If they were terribly enthusiastic, I suggested that they keep it as an avocation, but perhaps try to become a member of the faculty of a college or university and to use herpetology as their research

subject. Some of them did that, but most of the young people were just crestfallen.

It is very good for me to be back in Ohio. I've enjoyed every minute I've been here, and I have seen quite a little bit of this part of the state in the last few days. I became an employee of the Toledo Zoo in 1929. President Herbert Hoover and I started on the same day. I lasted a little longer than he did. I was there until 1935 and then I went back to Philadelphia, which was more or less my hometown. I had grown up and gone to school there. I enjoyed my work in Toledo very much. We were pioneering. Things happened there during the great depression that made the Toledo Zoo a world-class institution, which it certainly is today under the dynamic leadership of Bill Denner.

While I was in Toledo those six years I attempted to make a survey of the reptiles of Ohio. With my boon companions, young people in their teens, I traveled all over Ohio. We managed to do field work in 87 of the 88 counties. One of the places where we looked hard and long was the Pymatuning region. It was then the Pymatuning Swamp. In the 1930s it was being clear-cut in order to create the Pymatuning Reservoir. On the Pennsylvania side my colleagues had found the wood turtle and the bog turtle, neither of which had ever turned up in Ohio. Of course, we were very anxious to get over there and find one or both of those to add to the fauna of Ohio. Unfortunately, we never succeeded, but we tried year after year.

Nowadays it is possible to enter the Ohio turnpike near Toledo, drive to near Warren and then more or less diagonally upward to the northeastern corner of the state which is close to the Pymatuning. You can do that today in the matter of just a very few hours, but no such luxury existed back in the 1930s. The main road paralleled Lake Erie and went through every small town close to the lake, down the main street just as it had in horse and buggy days. So it took us a frightfully long time to get from Toledo to Cleveland. Our personal refueling stop in Cleveland was Childs' Restaurant which may now be long gone, but then it was open all night. We would go there and stuff ourselves with pancakes, sausages, scrambled eggs, donuts and cups of coffee, and then promptly go to sleep—except for the driver. Finally, after going

through an endless stream of suburbs on the eastern side of Cleveland we would emerge about dawn and see the milkman with his horse-drawn cart delivering milk to the houses. I'm sorry to say that in those days we thought of Cleveland as a horrible bottleneck to get through, and that was why we did it in the wee hours of the morning when there was little traffic.

I got back to Cleveland a number of times in the daylight and discovered it was a wonderful city. I was here many times. I went through the reptile collection at the old Museum of Natural History building and looked at all of the material, but there was not much of it. Of course, that building has long since disappeared. I came to know the zoo,

which was then a collection of barred cages and a monkey mountain. I have been able to look at your new building, this beautiful natural history museum, and my wife and I also spent a day at the zoo. What changes have taken place in the sixty years since I left Toledo. Certainly after tonight I will never forget Cleveland.

This wonderful honor which you have bestowed on me is an event that I'll remember always, and it is certainly a highlight of my long career. I extend my deepest thanks to all of you who had a part in it, those who supported me, to the trustees of the Museum, to Mary Taylor, and to Ray Novotny who was the catalyst who put it in motion. Thank you all for coming.



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MEMORIAL — SONJA E. TERAGUCHI (1941–1998)

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INVERTEBRATE ZOOLOGY

*CHECKLIST OF THE MOTHS OF PALLISTER STATE NATURE PRESERVE,
ASHTABULA COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE*

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Sonja E. Teraguchi and Katherine J. Lublin

*CHECKLIST OF THE MOTHS OF LAKE CARDINAL SWAMP,
ASHTABULA COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE*

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Sonja E. Teraguchi and Katherine J. Lublin

*CHECKLIST OF THE MOTHS OF GROVES WOODS PRESERVE,
TRUMBULL COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE*

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Sonja E. Teraguchi and Katherine J. Lublin

*CHECKLIST OF THE MOTHS OF GRAND RIVER TERRACES PRESERVE,
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*CHECKLIST OF THE MOTHS OF RESOURCES CENTER, HIDDEN VALLEY
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*CHECKLIST OF THE MOTHS OF WALDEN II NATURE PRESERVE,
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Sonja E. Teraguchi and Katherine J. Lublin

PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE

Miriam Smead, William C. McGrew, and Jane Goodall

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The Scientific Publication of The Cleveland Museum of Natural History

Joseph T. Hannibal, Editor

BRIEF HISTORY AND PURPOSE

Kirtlandia, a publication of The Cleveland Museum of Natural History, is named in honor of Jared Potter Kirtland, a noted nineteenth-century naturalist who lived in the Cleveland, Ohio area. It began publication in 1967 and is a continuation of the earlier series *Scientific Publications* volumes 1 to 10 (1928–1950), and new series volumes 1 to 4 (1962–1965).

Supported by the Kirtlandia Society of The Cleveland Museum of Natural History, *Kirtlandia* is devoted to the publication of scientific papers in the various fields of inquiry within the Museum's sphere of interest: Cultural and Physical Anthropology; Archaeology; Botany; Geology; Paleobotany; Invertebrate and Vertebrate Paleontology; Systematics; Ecology; and Invertebrate and Vertebrate Zoology. Issues will vary from single monographs to collections of short papers, review articles, and brief research notes.

Kirtlandia is abstracted in *Biological Abstracts* and indexed in *GeoRef* and *Zoological Record*.

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KIRTLANDIA

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SONJA E. TERAGUCHI (1941-1998)



You can't do science unless you have a mania for it. It takes so much work, you can't just do it nine to five; you have to put your body and soul into it. How far you get, how deep you get, how comprehensive your problem solving is — all of these depend on whether you're immersed in it.

Sonja Teraguchi (1997, p. 393)

Dr. Sonja Teraguchi was an entomologist and respected senior curator at The Cleveland Museum of Natural History. At the time of her death she was actively involved with a number of educational, curatorial, and scientific projects, notably a long-term study of the moth populations of northeastern Ohio. She also was a forceful local advocate for the preservation of the world's biological diversity.

Sonja Teraguchi was born in Kamloops, in southern British Columbia. Her life was influenced by the time she spent at her family's fishing camp on Shuswap Lake, where she became interested in nature. An interest in

entomology blossomed while she was an undergraduate student at the University of British Columbia. She majored in zoology, a field which she loved, as well as mathematics, a field that she pursued because of an influential high school teacher. Sonja obtained a bachelor's degree in zoology and mathematics in 1962, and was awarded a master's degree in zoology in 1964, from the University of British Columbia. She subsequently received a Ph.D. in zoology from the University of Wisconsin in 1972.

Sonja accompanied her husband, biologist Mitsuo Teraguchi, to Cleveland in 1970, and began work at Case Western Reserve University, first as a lecturer, and then as an assistant professor. She obtained a position at The Cleveland Museum of Natural History in 1974. Sonja would remain affiliated with Case Western Reserve as an adjunct faculty member until her death, but the heart of her work was at the Museum where she served as Curator of Invertebrate Zoology and was directly in charge of collections of insects, shells, and other invertebrates.

Dr. Teraguchi cared deeply about the Museum and its staff. She was administrative head of the curatorial division of the Museum in the 1980s. As such, she supervised the expansion of the curatorial staff and research collections, as well as the construction of additional space to house parts of the collections. Sonja spearheaded the computerization of the biological collections of the Museum, obtaining grants to fund the Museum's biological records program and working on various aspects of the program herself. She also served as a mentor to a number of young curators. Sonja worked on various exhibits as part of her duties at the Museum. At the time of her death, she had just completed work on an exhibit on organisms introduced into North America, including the European honeybee. This proved to be a great effort, and necessitated setting up honeybee colonies in her yard to supply bees for the live exhibit. This project stimulated an interest in apiculture.

Sonja was also an expert in forensic entomology, acting as a *pro bono* consultant for the Cuyahoga County Coroner's office. Her work included the identification of insects found on corpses and the training of police officers in the collection of these insects. She also consulted

on a wide variety of entomological projects, using any funds generated to subsidize her research program. Sonja was very generous with her time, fielding a great number of telephone questions from the general public, responding to numerous inquiries from members of the media, and examining a great number of insects and arachnids that arrived at the Museum in jars of all sizes.

Sonja took a great interest in students. She was instrumental in the formation of the Adopt-A-Student program at the Museum in 1980. That program, sponsored by the Kirtlandia Society, gives undergraduate students the opportunity to spend summers working on research projects with Museum curators. She spent a great deal of time administering this program, to the benefit of many students as well as most of the Museum's curators. During the last year of her life she had been active with what would ultimately be a successful effort to raise an endowment to help support the Adopt-A-Student Program.

Dr. Teraguchi was an advocate for the preservation of the world's biological diversity. Her efforts were primarily on the local level. They included her co-founding of the rainforest committee of the Northeast Ohio chapter of the Sierra Club and helping to organize conferences supported by the chapter. She also served on the Advisory Committee of the Earth Day Coalition.

Sonja was an active member of the Mentor Marsh Board of Management. She was also on the Nongame and Endangered Species Technical Advisory Committee of the Division of Wildlife of the Ohio Department of Natural Resources as well as the Ohio Gypsy Moth Management Council of the Ohio Department of Agriculture.

In the 1970s and 1980s, Dr. Teraguchi published on the negative buoyancy of the larva of the dipteran *Chaoborus americanus* (her thesis topic), the migration patterns and local movements of leafhoppers, and other topics. Her research program at the Museum initially focused on leafhoppers. By the end of the 1980s she began to turn most of her attention to butterflies and, especially, moths. She submitted a number of reports regarding gypsy moths and the preservation of biodiversity in Ohio to the Ohio Division of Wildlife and the Ohio Department of Agriculture.

During the past 13 years a great deal of Dr. Teraguchi's time was taken up with a long-term study of moths in northeastern Ohio. The study encompassed a number of sites in the watershed of the Grand River, many of these sites within The Cleveland Museum of Natural History's system of preserves. Her hope was that the long time frame of this study would allow for a mathematical analysis of these moth populations. She was also interested in what would happen to the native moth populations as the gypsy moth moved into this region, and what effect pesticides used to fight the gypsy moth would have on other species of moths. She was especially interested in the

effects of *Bacillus thuringiensis* on these nontarget moths. Sonja enlisted the aid of many students, including a number of students in the Adopt-A-Student program, and a core of dedicated volunteers to help with the herculean task of trapping, identifying, and curating some 45,000 moths per year. She insisted that her many specimens be properly curated so that they would be available to workers in the future. She also hoped that her work would eventually help planners make wise and informed decisions that would lead to the protection of moth species.

In recent years, Sonja had been helping to establish a long-term project monitoring Ohio's butterflies. This effort was patterned after a butterfly monitoring project in Great Britain. Through the efforts of Sonja and her colleagues, and with support of the Ohio Lepidopterists and the State of Ohio, 19 butterfly monitoring sites had been set up by 1998. It was intended that the data from these surveys would help to reveal the reasons for decline in various butterfly species. The project is ongoing.

Dr. Teraguchi was an associate editor of this journal. She was also the staff liaison to the Kirtlandia Society, which provides partial funding for this journal. In addition, Dr. Teraguchi served on the Editorial Committee of the Ohio Biological Survey and as a reviewer for the *Annals of the Entomological Society of America*.

Those interested in finding out more about Dr. Teraguchi's life should read her first-person account (Teraguchi, 1997), published in *Journeys of Women in Science and Engineering*. Although a modest person, she did take pride in having her biography included in this book, as she felt it could influence young women to pursue careers in the sciences. As her poignant words show, she was also very proud of being able to maintain a family and successfully raise two daughters while engaged in an intensive career in science. Of course, this did necessitate taking her daughters to the Museum to sort moths upon occasion! Her daughters are now grown. Sonja's husband, Mitsuo, died in 1991.

The six papers by S. Teraguchi and K. Lublin in this issue of *Kirtlandia* present only a portion of the data accumulated during Dr. Teraguchi's long-term moth study. These papers reflect the specimens and data collected during five years (1988–1992) of the study. All of the papers had passed through the review process shortly before Dr. Teraguchi's untimely death at the age of 57 in December of 1998. This issue of *Kirtlandia*, which includes six of the most comprehensive papers ever written on the moths of northeastern Ohio, stands as a memorial to her.

J. Hannibal

Reference

- Teraguchi, S. 1997. Sonja Teraguchi, p. 390–394. In S. A. Ambrose, K. L. Dunkle, B. B. Lazarus, I. Nair, and D. A. Harkus, *Journeys of Women in Science and Engineering: No Universal Constants*. Philadelphia, Temple University Press.

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CHECKLIST OF THE MOTHS OF PALLISTER STATE NATURE PRESERVE, ASHTABULA COUNTY, OHIO (1988-1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Pallister State Nature Preserve in Ashtabula County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988-1992) and includes 21,845 specimens representing 521 species. The study began in 1987 and continued through 1996, but only data for 1988-1992 are included here. The checklist is a historical record of the species that were present in 1988-1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after ten years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988-1992 is 6.71 and the Shannon-Wiener Evenness Index is 0.74. Two hundred seventeen of the 521 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. The less abundant species at Pallister are not less likely to be widespread than the more abundant species at Pallister, except for the singletons. Six species of owl moths that were collected at Pallister are of special interest in Ohio. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Description of the Surveillance Site at Pallister State Nature Preserve

Pallister State Nature Preserve is composed of 34 ha of forest and is bordered by Crooked Creek on the west and southwest, Callender Road on the north and a private residence on the east (Figure 1). It extends into Rome Township on the east and is part of a much larger forested area of approximately 1800 ha that extends 3 km north, south, and east (Anonymous, 1995). The Preserve is situated on swampy glacial lake plain with fine-grained lacustrine silt and clay soils (White and Totten, 1979, p. 7, Pl. 1) overlain by rich organic muck.

The light trap at Pallister State Nature Preserve was located in Hartsgrove Township in Ashtabula County on Callender Road at latitude 41° 38' 06" N and longitude 80° 54' 16" W (U.S. Geological Survey East Trumbull, Ohio, 7.5-minute quadrangle topographic map: Figure 1).

Pallister State Nature Preserve is located approximately 24 km east/northeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

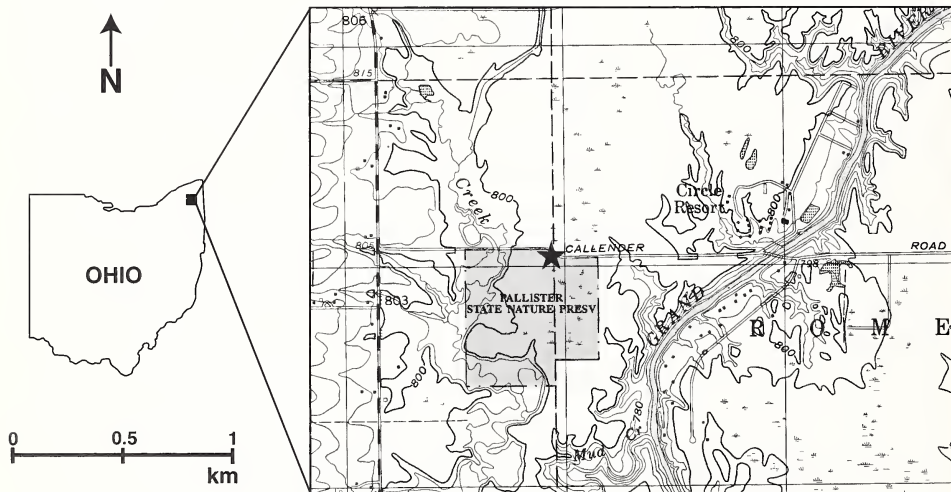


Figure 1. Map of the study area (adapted from the U.S. Geological Survey East Trumbull, Ohio, 7.5-minute quadrangle topographic map). Shaded area delineates Pallister State Nature Preserve; star indicates position of surveillance trap within the Preserve.

Table 1. Importance values for trees at the surveillance site at Pallister State Nature Preserve. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Tree Species		Canopy	Understory
Maple, red	<i>Acer rubrum</i> L.	126	0
Oak, white	<i>Quercus alba</i> L.	46	0
Cherry, black	<i>Prunus serotina</i> Ehrh.	41	26
Oak, swamp white	<i>Quercus bicolor</i> Willd.	26	0
Tupelo, black	<i>Nyssa sylvatica</i> Marsh.	25	31
Oak, northern red	<i>Quercus rubra</i> L.	20	42
Beech, American	<i>Fagus grandifolia</i> Ehrh.	7	112
Ash	<i>Fraxinus</i> spp.	7	25
Birch, yellow	<i>Betula alleghaniensis</i> Britt.	0	33
Hop Hornbeam, eastern	<i>Ostrya virginiana</i> (Mill.) K. Koch	0	12
Pine, eastern white	<i>Pinus strobus</i> L.	0	10
Hornbeam, American	<i>Carpinus caroliniana</i> Walt.	0	8

The composition of the canopy and understory was evaluated for the 2500 m² of forest centered on the surveillance trap (point-quarter technique, nine points; Cottam and Curtis, 1956; Cox 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90m at Pallister. The importance values for the trees at the surveillance site at Pallister State Nature Preserve are given in Table 1.

The herbaceous plants included: sedges *Carex seorsa* Howe and *Carex folliculata* L.; turtlehead *Chelone glabra* L.; ill-scented trillium *Trillium erectum* L.; creeping wintergreen *Gaultheria procumbens* L.; goldthread *Coptis trifolia* (L.) Salisb. ssp. *groenlandica* (Oeder) Hulten; *Dalibarda repens* L.; ferns *Osmunda cinnamomea* L. and *Osmunda regalis* L.; partridge berry *Mitchella repens* L.; cucumber root *Medeola virginiana* L.; false solomon's-seal *Smilacina racemosa* (L.); *Polygonum punctatum* Ell.; and *Utricularia minor* L. (James K. Bissell, 1998, personal communication; author citations according to Kartesz, 1994). *Utricularia minor* L. is listed as rare by the Ohio Division of Natural Areas and Preserves. These species were selected from a longer list of Pallister species on deposit in the Herbarium at The Cleveland Museum of Natural History. The surveillance trap was within 300 m of a pasture, within 300 m of a bog and within 300 m of a creek lined with aspens and willows.

Surveillance Techniques

One Ellisco®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, from late May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The

trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were computerized. All the specimens collected are deposited in the Insect Collection of The Cleveland Museum of Natural History.

Results and Discussion

A total of 21,845 specimens representing 521 species were collected in 1988–1992 (Appendix). Species were identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al. (1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodges et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 33 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1987 to 1996, is shown in Figure 2. In 1987 (not included in this checklist), 296 species were collected, and in 1996, after ten years, the total had reached 609 (1993–1996, also not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Pallister State Nature Preserve and five years would have been the minimum. The species accumulation curve was still rising after ten years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: fall, winter, and early spring moths are missing because collecting was not begun until the end of May and collecting ended in September. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

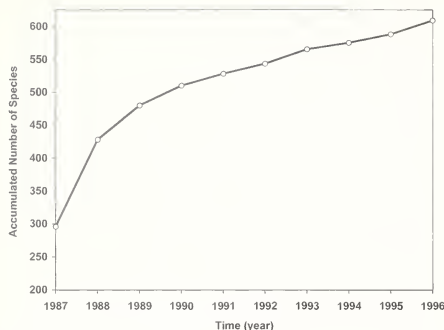


Figure 2. Plot of the annual accumulation of species collected at Pallister State Nature Preserve, 1987–1996.

Relative abundances of the 521 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The Shannon-Wiener Diversity Index is 6.71 and the Shannon-Wiener Evenness Index is 0.74.

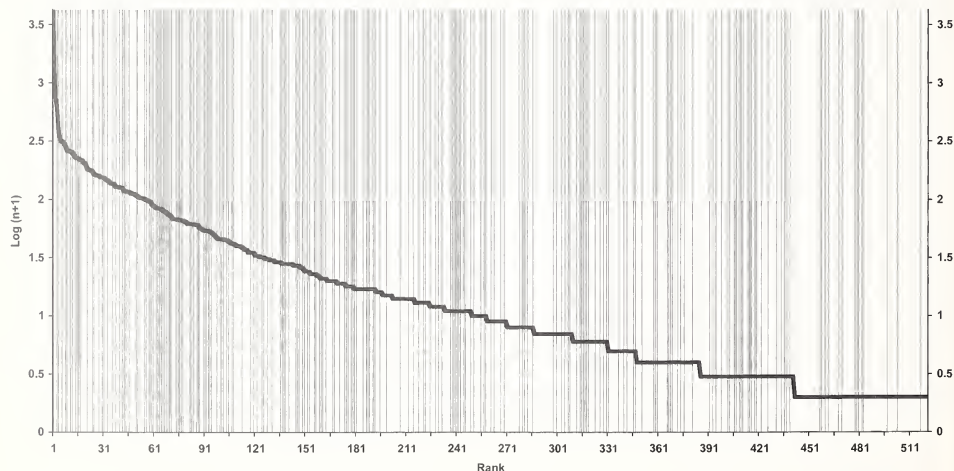


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Pallister State Nature Preserve, 1988–1992.

Almost 20 percent of the total count was composed of lesser maple spanworm moth *Itame pustularia* (6273), and red maple is the dominant canopy tree at this site. The next most abundant species was sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants. Following, in order of decreasing abundance, were: disparaged arches *Polia detrecta* (10288+), whose larva feeds on clover, blueberries, oaks, etc.; the banded tussock moth *Halysidota tessellaris* (8203+), whose larva feeds on many deciduous trees; the gypsy moth *Lymantria dispar* (8318) whose larva feeds on shrubs and trees, especially oak; the forest tent caterpillar moth *Malacosoma disstria* (7698) whose larva feeds on trees and shrubs, especially aspens and maples; the esther moth *Hypagyrtis esther* (6655) whose larva feeds on pines; the angulose prominent *Peridea angulosa* (7920) whose larva feeds on oaks; the large mossy lithacodia *Lithacodia muscosa* (9047) whose larva feeds on grasses; and the snowy geometer *Eugonobapta nivosaria* (6965) whose larval host is unrecorded.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 217 Pallister species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988, 1990). Three explanations have been proposed (Krebs, 1994).

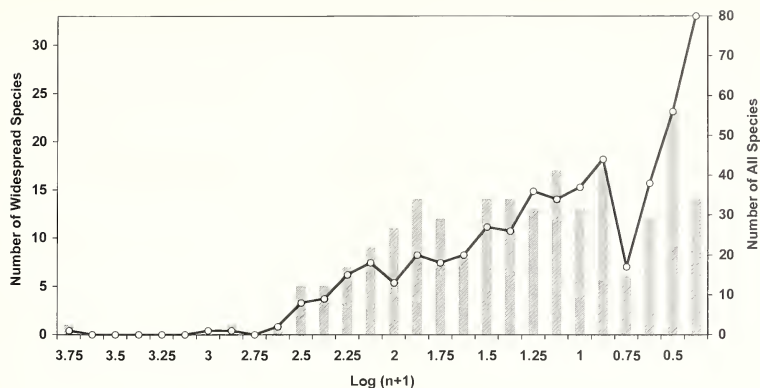


Figure 4. Correspondence between the total number of Pallister species in an abundance interval (line scale at right) and the number of widespread Pallister species in the same abundance interval (bar scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

First, the relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not exist when abundance is viewed from the perspective of abundance at Pallister. Of the 217 Pallister species which are widespread in northeast Ohio, 95 had total counts of 10 or fewer at Pallister.

Overall, there is a close correspondence between the number of widespread species in an abundance interval and the total number of species (Figure 4). Only the decrease in the proportion of widespread species in the singleton interval conforms to expectation. The 80 singleton species at Pallister include only 14 widespread species, whereas the 56 doubleton species include 23 widespread species. The less abundant species at Pallister are not less likely to be widespread than the more abundant species with the exception of the singleton species which are less likely to be widespread.

Six species of owl moths collected at Pallister are listed as being of special interest in Rings et al. (1992): *Papaipema nepheleptena* (9490) whose larva bores in turtlehead; *Enargia decolor* (9549) whose larva feeds on trembling aspen, speckled alder, and willow; *Enargia infumata* (9550) whose larva feeds on trembling aspen and willow; puta sawfly *Anathix puta* (9962), whose larva feeds on trembling aspen; stormy arches *Polia umbrosa* (10275) whose larva feeds on alder and huckleberries; and scurvy quaker *Homorhodes fufurata* (10532) whose larva feeds on maples. One species, *Enois occulta* (10929)

whose larva feeds on birch and willow, is listed as status unknown. All of these host plants are present at Pallister.

Acknowledgments

A huge debt is owed to E. Metzler of The Ohio Lepidopterists for intensive training and extensive help with identifications. More than 15 students helped with all parts of the project, especially P. Fuchsmann, P. Ferreri, E. Chapman, and R. Bartholomew. G. McCarty was instrumental in getting the computerization process underway. Financial support was received from the Ohio Division of Wildlife, the United States Forest Service, the Pack Foundation, the Storer Foundation, The Kirtlandia Society, and The Cleveland Museum of Natural History. We gratefully acknowledge assistance from D. Horn, Professor of Entomology at the Ohio State University, in securing funding. We thank E. Metzler and R. Rings for critically reviewing the manuscript.

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Appendix. Checklist of species collected at Pallister State Nature Preserve, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection, and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family HEPIALIDAE		3633	<i>Choristoneura parallela</i> (Rob.)
20	<i>Sthenopis quadriguttatus</i> (Grt.)		June 15, 1988–Aug. 16, 1990 Count 10
	July 4, 1989–July 15, 1988 Count 3	3635	<i>Choristoneura rosaceana</i> (Harr.)
Family OECOPHORIDAE			June 12, 1992–Sep. 14, 1990 Count 102
882	<i>Agonopterix robinella</i> (Pack.)	3648	<i>Archips argyrosipila</i> (Wlk.)
	Aug. 26, 1988 Count 1		June 22, 1990–June 29, 1988 Count 6
951	<i>Machimia tentoriferella</i> Clem.	3655	<i>Archips fervidana</i> (Clem.)
	Sep. 10, 1988 Count 1		July 4, 1989 Count 2
957	<i>Psilocorsis reflexella</i> Clem.	3672	<i>Syndemis afflictana</i> (Wlk.)
	June 1–Aug. 5, 1988 Count 111		May 18, 1988 Count 2
1014+	<i>Antaeotricha leucillana</i> (Zell.)	3686	<i>Clepsis melaleucana</i> (Wlk.)
	May 21, 1989–Aug. 31, 1990 Count 254		June 1, 1988–July 3, 1992 Count 29
1046	<i>Callima argenticinctella</i> Clem.	3695	<i>Sparganothis sulfureana</i> (Clem.)
	June 22, 1990 Count 2		July 4, 1989 Count 1
Family GELECHIIDAE		3720	<i>Sparganothis reticulatana</i> (Clem.)
2295	<i>Trichotaphe flavocostella</i> (Clem.)		June 22–Aug. 5, 1988 Count 9
	July 10, 1989 Count 1	3725	<i>Sparganothis petitiiana</i> (Rob.)
Family YPONOMEUTIDAE			June 13, 1991–July 24, 1989 Count 6
2420	<i>Yponomeuta multipunctella</i> Clem.	Family LIMACODIDAE	
	June 20, 1991–Aug. 26, 1988 Count 161	4652	<i>Tortricidia testacea</i> Pack.
Family SESHIDAE			June 1, 1990–July 15, 1988 Count 65
2554	<i>Synanthedon acerni</i> (Clem.)	4654	<i>Tortricidia flexuosa</i> (Grt.)
	June 6, 1991–Sep. 25, 1992 Count 3		May 28, 1992–July 27, 1990 Count 177
Family COSSIDAE		4659	<i>Packardia geminata</i> (Pack.)
2693	<i>Prionoxystus robiniae</i> (Peck)		June 1, 1988–July 10, 1992 Count 27
	June 15, 1988 Count 1	4661	<i>Packardia elegans</i> (Pack.)
Family TORTRICIDAE			June 6, 1991–July 10, 1992 Count 23
2863	<i>Hedya chionosema</i> (Zell.)	4665	<i>Lithacodes fasciola</i> (H.-S.)
	Aug. 5, 1988 Count 1		June 6, 1991–Aug. 7, 1992 Count 39
3186	<i>Epiblema scudderiana</i> (Clem.)	4667	<i>Apoda y-inversum</i> (Pack.)
	June 15, 1988 Count 1		June 22, 1988–July 20, 1990 Count 10
3361	<i>Ancylis semiovana</i> (Zell.)	4669	<i>Apoda biguttata</i> (Pack.)
	June 1–Aug. 19, 1988 Count 13		June 6, 1991–Aug. 5, 1988 Count 13
3494	<i>Melissopus latiferreanus</i> (Wlsm.)	4671	<i>Prolimacodes badia</i> (Hbn.)
	Aug. 14, 1989 Count 2		June 27, 1991–July 22, 1988 Count 4
3503	<i>Croesia semipurpurana</i> (Kft.)	4681	<i>Isa textula</i> (H.-S.)
	June 22, 1988–June 26, 1989 Count 7		June 20, 1991–July 10, 1989 Count 6
3594	<i>Pandemis limitata</i> (Rob.)	4685	<i>Adoneta spinuloides</i> (H.-S.)
	June 8–Aug. 31, 1990 Count 20		June 20, 1991–July 20, 1990 Count 4
3623	<i>Argyrotaenia quercifoliana</i> (Fitch)	4697	<i>Encleia delphinii</i> (Bdv.)
	June 6, 1991–July 31, 1992 Count 125		May 30–June 27, 1991 Count 11
3624	<i>Argyrotaenia alisellana</i> (Rob.)	Family CRAMBIDAE	
	June 6, 1991–July 3, 1992 Count 116	4703	<i>Gesneria centuriella</i> (D. & S.)
3625	<i>Argyrotaenia mariana</i> (Fern.)		June 4, 1989–July 22, 1988 Count 37
	May 18, 1988 Count 2	4748	<i>Munroessa iccissalis</i> (Wlk.)
3632	<i>Choristoneura fractivittana</i> (Clem.)		June 8, 1990–Aug. 27, 1992 Count 102
	May 30, 1991–June 26, 1992 Count 160	4749	<i>Munroessa faulalis</i> (Wlk.)
			July 24, 1989–Aug. 27, 1992 Count 4
		4751	<i>Munroessa gyralis</i> (Hulst)
			June 15, 1988–Sep. 9, 1989 Count 30

4755	<i>Synclita oblitalis</i> (Wlk.) June 8, 1990–Aug. 14, 1989	Count 3
4889	<i>Dicynolomia julianalis</i> (Wlk.) July 3, 1992–Sep. 7, 1990	Count 6
4897	<i>Evergestis pallidata</i> (Hufn.) May 30, 1991–Sep. 10, 1988	Count 31
4936	<i>Saurobotrys futilalis</i> (Led.) Aug. 2–Aug. 30, 1991	Count 10
4937	<i>Nascia acutella</i> (Wlk.) June 29, 1990–Aug. 2, 1991	Count 6
4944	<i>Crocidophora serratissimalis</i> Zell. June 1–Sep. 10, 1988	Count 206
4945	<i>Crocidophora tubercularis</i> Led. June 15, 1988–Aug. 21, 1989	Count 61
4949	<i>Ostrinia nubilalis</i> (Hbn.) June 1, 1988–Aug. 27, 1992	Count 20
4950	<i>Fumibotrys funalis</i> (Gn.) July 12, 1991–Aug. 14, 1989	Count 5
4951	<i>Perispasta caecalis</i> Zell. June 1, 1990–July 31, 1989	Count 7
4952	<i>Eurhyphara hortulata</i> (L.) June 26, 1989	Count 1
4953a	<i>Phlyctaenia coronata terialis</i> (Gn.) May 30, 1991–Aug. 27, 1992	Count 19
4962	<i>Hahncappisia maculenta</i> (G. & R.) June 1, 1988–Aug. 21, 1989	Count 8
5040	<i>Pyrausta bicoloralis</i> (Gn.) June 26, 1989–Sep. 13, 1991	Count 44
5071	<i>Pyrausta acronialis</i> (Wlk.) June 20, 1991–Sep. 2, 1989	Count 26
5079	<i>Udea rubigalis</i> (Gn.) May 28, 1989–Sep. 13, 1991	Count 60
5142	<i>Diaene elealis</i> (Wlk.) July 5, 1991–Aug. 7, 1992	Count 67
5156	<i>Nomophila nearctica</i> Mun. July 19–Aug. 30, 1991	Count 6
5159	<i>Desmia funeralis</i> (Hbn.) June 12, 1992–Sep. 7, 1990	Count 16
5182	<i>Blepharomastix raulalis</i> (Gn.) June 26, 1989–July 22, 1988	Count 2
5226	<i>Palpia magniferalis</i> (Wlk.) May 30–Aug. 2, 1991	Count 39
5228	<i>Polygrammodes flavidalis</i> (Gn.) June 19, 1989–Aug. 26, 1988	Count 65
5233	<i>Compacta capitalis</i> (Grt.) June 15, 1988	Count 1
5241	<i>Pantographa lineata</i> (G. & R.) June 27, 1991–Aug. 27, 1992	Count 77
5272	<i>Herpetogramma bipunctalis</i> (F.) June 15, 1988–Aug. 14, 1989	Count 55
5275	<i>Herpetogramma pertextalis</i> (Led.) June 26–Aug. 21, 1989	Count 50
5280	<i>Herpetogramma aeglealis</i> (Wlk.) June 12, 1992–Aug. 2, 1991	Count 20
5281	<i>Pilocrocis ramentalis</i> Led. July 5, 1991–July 31, 1989	Count 22
5362+	<i>Crambus agitatellus</i> Clem. June 15, 1988–Sep. 9, 1989	Count 779

5420	<i>Microcrambus elegans</i> (Clem.) July 8, 1988	Count 1
5464	<i>Urola nivalis</i> (Drury) June 20, 1991–July 22, 1988	Count 18
5465	<i>Vaxi auratella</i> (Clem.) July 20–Aug. 3, 1990	Count 8
5497	<i>Eoreuma callista</i> Klotz July 3, 1992	Count 2

Family PYRALIDAE

5510	<i>Pyralis farinalis</i> L. July 8, 1988	Count 1
5518	<i>Aglossa cuprina</i> Zell. June 20, 1991–Aug. 31, 1990	Count 179
5524	<i>Hypsopygia costalis</i> (F.) June 22–July 22, 1988	Count 9
5532	<i>Herculia infimbrialis</i> Dyar July 24, 1989–Aug. 24, 1990	Count 6
5533	<i>Herculia olinalis</i> (Gn.) July 3–Aug. 27, 1992	Count 3
5552	<i>Galasa nigrinodis</i> (Zell.) July 5, 1991–Sep. 10, 1988	Count 4
5556	<i>Tosale oviplagalis</i> (Wlk.) June 20, 1991–July 10, 1989	Count 4
5571	<i>Condylolomia partipialis</i> Grt. June 29–July 20, 1990	Count 11
5577	<i>Epipaschia superatalis</i> Clem. June 20, 1991–Aug. 3, 1990	Count 9
5606	<i>Tetralopha asperatella</i> (Clem.) Aug. 9, 1990	Count 1
5997	<i>Euzophera ostricorella</i> Hulst June 26, 1989–Sep. 7, 1990	Count 7
6053	<i>Peoria approximella</i> (Wlk.) June 19, 1992–July 20, 1990	Count 7

Family THYRIDIDAE

6079	<i>Dysodia granulata</i> (Neum.) Aug. 5, 1988	Count 1
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Family THYATIRIDAE

6237	<i>Pseudothyrtaria cymatophoroides</i> (Gn.) Aug. 5, 1988–Sep. 14, 1990	Count 2
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Family DREPANIDAE

6251	<i>Drepana arcuata</i> Wlk. May 30, 1991–Aug. 5, 1988	Count 4
6253	<i>Endeileiia herminata</i> (Gn.) June 29, 1988–Aug. 9, 1990	Count 2
6255	<i>Oreta rosca</i> (Wlk.) May 30, 1991–Sep. 9, 1989	Count 82

Family GEOMETRIDAE

6261	<i>Heliomata cycladota</i> G. & R. June 15, 1988–July 3, 1992	Count 2
6270	<i>Protitame virginialis</i> (Hulst) June 15, 1988–Aug. 14, 1989	Count 12
6272	<i>Eumacaria latiferrugata</i> (Wlk.) Aug. 3, 1990	Count 1
6273	<i>Itame pustularia</i> (Gn.) June 13, 1991–Sep. 9, 1989	Count 4275

6299	<i>Itame coortaria</i> (Hulst) June 13, 1991–July 17, 1989.	Count 21	6739	<i>Euchlaena irraria</i> (B. & McD.) June 15, 1988.	Count 1
6303	<i>Itame subcessaria</i> (Wlk.) July 17–July 24, 1989.	Count 3	6740+	<i>Xanthotype urticaria</i> Swett May 30, 1991–Sep. 2, 1989.	Count 31
6335+	<i>Semiothisa aequiferaria</i> (Wlk.) May 30, 1991–Aug. 24, 1990.	Count 61	6753+	<i>Pero honestaria</i> (Wlk.) May 21, 1989–Aug. 27, 1992.	Count 108
6340	<i>Semiothisa minorata</i> (Pack.) Aug. 5, 1988.	Count 1	6763	<i>Nacophora quernaria</i> (J.E. Smith) June 1, 1990.	Count 1
6342	<i>Semiothisa bisignata</i> (Wlk.) June 8, 1990–Aug. 5, 1988.	Count 22	6796	<i>Campaea perlata</i> (Gn.) May 30, 1991–Sep. 24, 1988.	Count 230
6344+	<i>Semiothisa signaria</i> (Hbn.) May 30, 1991–Aug. 16, 1990.	Count 10	6797	<i>Ennomos magnaria</i> Gn. Aug. 14–Sep. 2, 1989.	Count 2
6386	<i>Semiothisa ocellinata</i> (Gn.) July 10, 1989.	Count 2	6798	<i>Ennomos subsignaria</i> (Hbn.) June 20, 1991–Aug. 21, 1992.	Count 147
6405	<i>Semiothisa gnophosaria</i> (Gn.) July 4, 1989–July 12, 1991.	Count 3	6819	<i>Metanema inatomaia</i> Gn. June 15, 1988–Aug. 16, 1990.	Count 6
6582	<i>Anacamptodes vellivolata</i> (Hulst) June 1, 1988.	Count 6	6820	<i>Metanema determinata</i> Wlk. July 5, 1991.	Count 2
6583	<i>Anacamptodes ephyriaria</i> (Wlk.) June 20, 1991–July 24, 1989.	Count 127	6822	<i>Metarranthis dharia</i> (Gn.) May 28, 1989.	Count 1
6584	<i>Anacamptodes humaria</i> (Gn.) June 20, 1991–July 31, 1989.	Count 5	6823	<i>Metarranthis angularia</i> B. & McD. June 22, 1988–July 3, 1992.	Count 3
6586	<i>Anacamptodes defectaria</i> (Gn.) July 6, 1990.	Count 2	6825	<i>Metarranthis indeclinata</i> (Wlk.) June 5–June 19, 1992.	Count 13
6588	<i>Iridopsis larvaria</i> (Gn.) May 21, 1989–Aug. 19, 1988.	Count 26	6826	<i>Metarranthis hypocharia</i> (H.-S.) June 1, 1988–July 3, 1992.	Count 106
6590	<i>Anavitrinella pampinaria</i> (Gn.) June 1, 1988–Sep. 13, 1991.	Count 53	6827	<i>Metarranthis refractaria</i> (Gn.) July 10, 1992.	Count 2
6597	<i>Ectropis crepuscularia</i> (D. & S.) June 6, 1991–Aug. 21, 1992.	Count 99	6828	<i>Metarranthis homuraria</i> (G. & R.) June 8–June 22, 1988.	Count 2
6598	<i>Protoaboarmia porcelaria</i> (Gn.) June 5, 1992–Sep. 10, 1988.	Count 14	6835	<i>Cepphis armataria</i> (H.-S.) June 15–July 22, 1988.	Count 6
6599	<i>Epimecis hortaria</i> (F.) May 28, 1992–Sep. 14, 1990.	Count 43	6836	<i>Anagoga occiduaris</i> (Wlk.) July 24–Aug. 14, 1989.	Count 17
6620+	<i>Melanolophia canadaria</i> (Gn.) May 18, 1988–Sep. 14, 1990.	Count 217	6838+	<i>Probole amicaria</i> (H.-S.) May 28, 1992–Aug. 9, 1990.	Count 146
6638	<i>Eufidonia notataria</i> (Wlk.) June 12, 1989.	Count 1	6840	<i>Plagodis serinaria</i> H.-S. May 18, 1988–July 3, 1992.	Count 182
6640a	<i>Biston bendaria cognataria</i> (Gn.) Aug. 2, 1991.	Count 1	6841	<i>Plagodis kuetzingi</i> (Grt.) June 1, 1988.	Count 2
6654	<i>Hypagyrtis unipunctata</i> (Haw.) June 1–Aug. 24, 1990.	Count 27	6843	<i>Plagodis fervidaria</i> (H.-S.) July 24, 1989–Aug. 5, 1988.	Count 6
6655	<i>Hypagyrtis esther</i> (Barnes) May 30, 1991–Sep. 7, 1990.	Count 309	6844	<i>Plagodis alcoalaria</i> (Gn.) May 18, 1988–Aug. 7, 1989.	Count 88
6667	<i>Lomographa vestaliata</i> (Gn.) May 28, 1992–July 17, 1989.	Count 56	6863	<i>Caripeta divisata</i> Wlk. June 22, 1988–Aug. 16, 1990.	Count 3
6677	<i>Cabera erythemaria</i> Gn. May 30, 1991–Sep. 9, 1989.	Count 87	6884	<i>Besma endropiaria</i> (G. & R.) May 30, 1991–Aug. 21, 1992.	Count 45
6678	<i>Cabera variolaria</i> Gn. June 12–Aug. 21, 1989.	Count 7	6885	<i>Besma quercivoraria</i> (Gn.) May 18, 1988–Sep. 9, 1989.	Count 80
6720	<i>Lytrosia unitaria</i> (H.-S.) June 13, 1991–July 10, 1989.	Count 97	6888	<i>Lambdina fiscellaria</i> (Gn.) Sep. 6, 1991–Sep. 25, 1992.	Count 15
6724	<i>Euchlaena serrata</i> (Drury) June 20, 1991–July 10, 1989.	Count 6	6894a	<i>Lambdina fervidaria athasaria</i> (Wlk.) July 12, 1991–Aug. 27, 1992.	Count 3
6725	<i>Euchlaena muzaria</i> (Wlk.) June 30, 1991–July 24, 1989.	Count 64	6912	<i>Sicya macularia</i> (Harr.) June 13, 1991–July 10, 1989.	Count 34
6729	<i>Euchlaena johnsonaria</i> (Fitch) June 15, 1988–Aug. 21, 1989.	Count 10	6941	<i>Enisarca confusaria</i> Hbn. June 20, 1991–July 24, 1989.	Count 34

6963	<i>Tetracis crocallata</i> Gn. July 3–July 10, 1992	Count 2
6964	<i>Tetracis cachexiata</i> Gn. May 30, 1991–June 26, 1992.	Count 153
6965	<i>Eugonobapta nivosaria</i> (Gn.) June 20, 1991–July 31, 1992.	Count 258
6966	<i>Eutrapela clemataria</i> (J.E. Smith) May 18, 1988–Aug. 21, 1989	Count 127
6982	<i>Prochoerodes transversata</i> (Drury) June 20, 1991–Sep. 24, 1988.	Count 95
6987	<i>Antepione thisoaria</i> (Gn.) July 4–July 31, 1989	Count 5
7009	<i>Nematocampa limbata</i> (Haw.) June 6, 1991–Sep. 9, 1989.	Count 154
7046+	<i>Nemoria bistriaria</i> Hbn. July 12, 1991–Aug. 27, 1992.	Count 53
7047	<i>Nemoria rubrifrontaria</i> (Pack.) June 1, 1988.	Count 2
7048	<i>Nemoria nimosaria</i> (Gn.) May 28–Aug. 27, 1992	Count 9
7053	<i>Dichorda iridaria</i> (Gn.) May 28–Aug. 14, 1989	Count 4
7058	<i>Synchlora aerata</i> (F.) June 22, 1988–Sep. 13, 1991.	Count 12
7071	<i>Chlorochlamys chloroleucaria</i> (Gn.) June 5–Aug. 27, 1992	Count 5
7132	<i>Pleuroprucha insularia</i> (Gn.) June 22, 1988–Sep. 14, 1990.	Count 13
7136	<i>Cyclophora packardii</i> (Prout) July 1–Sep. 21, 1990.	Count 32
7139	<i>Cyclophora pendulinaria</i> (Gn.) July 12, 1991–Sep. 2, 1989.	Count 4
7157	<i>Scopula cacuminaria</i> (Morr.) June 12, 1992–Aug. 31, 1990	Count 25
7159	<i>Scopula limboundata</i> (Haw.) June 15, 1988–Aug. 21, 1989	Count 153
7169	<i>Scopula inductata</i> (Gn.) June 12–Aug. 14, 1989	Count 11
7189	<i>Dysstroma herstiliata</i> (Gn.) June 26, 1989–June 27, 1991.	Count 2
7196+	<i>Eulithis diversilineata</i> (Hbn.) June 27, 1991–Sep. 10, 1988.	Count 23
7236+	<i>Hydriomena renunciata</i> (Wlk.) May 18, 1988.	Count 1
7292	<i>Hydria prunivora</i> (Fgn.) June 1–July 8, 1988.	Count 2
7368	<i>Xanthorhoe labradorensis</i> (Pack.) Aug. 19, 1988–Sep. 25, 1992.	Count 9
7388	<i>Xanthorhoe ferrugata</i> (Cl.) June 1–Sep. 10, 1988.	Count 6
7390	<i>Xanthorhoe lacustrata</i> (Gn.) June 1, 1990–Aug. 27, 1992.	Count 13
7394	<i>Epirrhoe alternata</i> (Muller) June 1, 1990–Aug. 30, 1991	Count 7
7399a	<i>Euphyia unangulata intermediata</i> (Gn.) May 30, 1991–Sep. 10, 1988.	Count 27
7414	<i>Orthonama obstripata</i> (F.) June 6, 1991–Aug. 24, 1990.	Count 42

7416	<i>Orthonama centrostrigaria</i> (Woll.) May 30–Sep. 6, 1991.	Count 117
7422	<i>Hydrelia inornata</i> (Hulst) June 12, 1992.	Count 1
7423	<i>Hydrelia albifera</i> (Wlk.) June 12–Aug. 7, 1989	Count 7
7430	<i>Trichodezia albiovittata</i> (Gn.) July 5, 1991–Aug. 5, 1988.	Count 2
7440	<i>Eubaphe mendica</i> (Wlk.) June 6, 1991–July 22, 1988.	Count 20
7445	<i>Horisme intestinata</i> (Gn.) June 8, 1990–Sep. 9, 1989.	Count 28
7474+	<i>Eupithecia miserulata</i> Grt. May 21, 1989–Sep. 14, 1990.	Count 137
7640	<i>Lobophora nivergerata</i> Wlk. June 15–June 22, 1988.	Count 2
7647	<i>Heterophleps triguttaria</i> H.-S. June 15, 1990–July 31, 1989.	Count 7
7648	<i>Dyspteris abortivaria</i> (H.-S.) June 15, 1988.	Count 1

Family EPIPLEMIDAE

7653	<i>Calledapteryx dryopterata</i> Grt June 20, 1991–Aug. 16, 1990.	Count 4
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Family MIMALLONIDAE

7659	<i>Lacosoma chiridota</i> Grt. June 15, 1988.	Count 1
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Family APATELODIDAE

7663	<i>Apateledes torrefacta</i> (J.E. Smith) June 6, 1991–July 15, 1988.	Count 12
7665	<i>Olceclostera angelica</i> (Grt.) June 6, 1991–July 20, 1990.	Count 5

Family LASIOCAMPIDAE

7670	<i>Tolyte vellela</i> (Stoll) Sep. 6, 1991–Sep. 24, 1988.	Count 32
7687	<i>Phyllodesma americana</i> (Harr.) June 27, 1991– July 15, 1988.	Count 3
7698	<i>Malacosoma dissrria</i> Hbn. June 20, 1991–Aug. 5, 1988.	Count 313
7701	<i>Malacosoma americanum</i> (F.) June 20, 1991–July 17, 1989.	Count 115

Family SATURNIIDAE

7715	<i>Dryocampa rubicunda</i> (F.) May 30, 1991–July 17, 1992.	Count 29
7723	<i>Anisota virginienis</i> (Drury) July 10, 1989.	Count 1
7746	<i>Automeris io</i> (F.) May 30, 1991–June 26, 1989.	Count 10
7757	<i>Antheraea polyphemus</i> (Cram.) June 26, 1992–July 12, 1991.	Count 4
7758	<i>Actias luna</i> (L.) June 1, 1990–July 4, 1989.	Count 5

Family SPHINGIDAE

7787	<i>Ceratonia undulosa</i> (Wlk.) June 29–July 27, 1990.	Count 3
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7810	<i>Sphinx gordius</i> Cram. June 1, 1990.....	Count 1
7821	<i>Suerinthus jamaicensis</i> (Drury) May 30, 1991–Aug. 9, 1990.....	Count 3
7824	<i>Paonias excaecatus</i> (J.E. Smith) May 30, 1991–Aug. 5, 1988.....	Count 54
7825	<i>Paonias myops</i> (J.E. Smith) June 6, 1991–Aug. 14, 1989.....	Count 11
7827	<i>Laothoe juglandis</i> (J.E. Smith) May 30, 1991–July 15, 1988.....	Count 7
7871	<i>Deidamia inscripta</i> (Harr.) May 28, 1989.....	Count 2
7886	<i>Darapsa pholis</i> (Cram.) June 6, 1991–July 22, 1988.....	Count 3

Family NOTODONTIDAE

7895	<i>Clostera albosigna</i> Fitch May 28–Sep. 2, 1989.....	Count 16
7896	<i>Clostera inclusa</i> (Hbn.) Aug. 3, 1990.....	Count 1
7898	<i>Clostera strigosa</i> (Grt.) May 28, 1989–July 27, 1990.....	Count 16
7901	<i>Clostera apicalis</i> (Wlk.) July 5, 1991–Aug. 7, 1992.....	Count 10
7902	<i>Datana ministra</i> (Drury) June 29, 1988–July 20, 1990.....	Count 5
7903	<i>Datana angustii</i> G. & R. June 27, 1991–July 29, 1988.....	Count 5
7904+	<i>Datana drexlii</i> Hy. Edw. July 10, 1989–July 27, 1990.....	Count 13
7906+	<i>Datana contracta</i> Wlk. June 27, 1991–July 22, 1988.....	Count 5
7915	<i>Nadata gibbosa</i> (J.E. Smith) May 28, 1989–Aug. 27, 1992.....	Count 257
7917	<i>Hyperaeschra georgica</i> (H.-S.) May 30, 1991.....	Count 2
7919	<i>Peridea bastiricus</i> (Wlk.) May 30, 1991–July 29, 1988.....	Count 21
7920	<i>Peridea angulosa</i> (J.E. Smith) May 30, 1991–Sep. 9, 1989.....	Count 290
7922	<i>Pheosia rimosus</i> Pack. June 1, 1990–Sep. 9, 1989.....	Count 18
7924	<i>Odontotia elegans</i> (Stkr.) July 15, 1988.....	Count 1
7926	<i>Notodontia scitipennis</i> Wlk. July 19, 1991–Aug. 3, 1990.....	Count 3
7929	<i>Nerice bidentata</i> Wlk. June 1–Aug. 16, 1990.....	Count 10
7930	<i>Ellida caniplaga</i> (Wlk.) June 15, 1988–July 13, 1990.....	Count 7
7931	<i>Gluphisia septentrionis</i> Wlk. May 30, 1991–July 24, 1989.....	Count 7
7936	<i>Furcula borealis</i> (Guer.-Meneville) Aug. 5, 1988.....	Count 1
7951+	<i>Symmerista albifrons</i> (J.E. Smith) May 30, 1991–Aug. 16, 1990.....	Count 125
7957	<i>Dasylophia anguina</i> (J.E. Smith) June 15, 1990–Aug. 14, 1989.....	Count 4
7958	<i>Dasylophia thyatiroides</i> (Wlk.) June 1–Aug. 26, 1988.....	Count 10

7975	<i>Macnurocampa marthesia</i> (Cram.) June 20, 1991–Aug. 9, 1990.....	Count 117
7994	<i>Heterocampa guttivitta</i> (Wlk.) May 28, 1989–July 22, 1988.....	Count 136
7995	<i>Heterocampa bimdata</i> Wlk. May 30, 1991–Aug. 27, 1992.....	Count 16
7998	<i>Lochmaeus manteo</i> Doubleday July 13–Aug. 9, 1990.....	Count 26
7999	<i>Lochmaeus bilineata</i> (Pack.) June 1–Aug. 19, 1988.....	Count 26
8005	<i>Schizura ipomoeae</i> Doubleday May 30–Aug. 16, 1991.....	Count 10
8006	<i>Schizura badia</i> (Pack.) June 1, 1988–Aug. 9, 1990.....	Count 13
8007	<i>Schizura unicoloris</i> (J.E. Smith) June 5, 1992–Aug. 31, 1990.....	Count 66
8011	<i>Schizura leptinoides</i> (Grt.) June 15, 1990–Aug. 5, 1988.....	Count 8
8012	<i>Oligocentria semirufescens</i> (Wlk.) June 20, 1991–July 17, 1989.....	Count 3
8017	<i>Oligocentria ligulicolor</i> (Wlk.) July 22, 1988–Aug. 16, 1990.....	Count 5

Family ARCTIIDAE

8045.1	<i>Crambidia pallida</i> Pack. July 24, 1989–Aug. 31, 1990.....	Count 18
8090	<i>Hypoprepia fucosa</i> Hbn. June 27, 1991–Aug. 16, 1990.....	Count 242
8104	<i>Comachata cadburyi</i> Franc. June 12, 1992.....	Count 1
8107	<i>Haploa clymene</i> (Brown) July 12, 1991–Aug. 7, 1992.....	Count 14
8121+	<i>Holonetina aurantiaca</i> (Hbn.) June 6, 1991–Aug. 9, 1990.....	Count 216
8129	<i>Pyrrharctia isabella</i> (J.E. Smith) May 30, 1991–Aug. 24, 1990.....	Count 23
8133	<i>Spilosoma latipennis</i> Stretch June 1, 1988–July 3, 1992.....	Count 16
8134	<i>Spilosoma congrua</i> Wlk. May 28, 1989–Aug. 2, 1991.....	Count 164
8137	<i>Spilosoma virginica</i> (F.) June 1, 1990–Sep. 6, 1991.....	Count 46
8140	<i>Hyphautria cinea</i> (Drury) June 20, 1991–July 10, 1992.....	Count 2
8156	<i>Phragmatobia fuliginosa</i> (L.) July 12, 1991–July 31, 1989.....	Count 8
8169+	<i>Apantesis phalerata</i> (Harr.) June 12, 1992–Aug. 21, 1989.....	Count 14
8197	<i>Apantesis virgo</i> (L.) July 17–July 24, 1989.....	Count 4
8203+	<i>Halysidota tessellaris</i> (J.E. Smith) June 6, 1991–Aug. 7, 1992.....	Count 387
8211	<i>Lophocampa caryae</i> Harr. May 30, 1991–June 15, 1988.....	Count 45
8214	<i>Lophocampa maculata</i> Harr. May 30, 1991.....	Count 1
8230	<i>Cycnia tenera</i> Hbn. June 15, 1988–July 13, 1990.....	Count 9
8231	<i>Cycnia oregonensis</i> (Stretch) July 29, 1988.....	Count 1

- 8238 *Euchaetes egle* (Drury)
June 20, 1991–July 24, 1989 Count 13
- 8262 *Ctenucha virginica* (Esp.)
June 12, 1989–June 15, 1988 Count 3
- 8267 *Ciseps fulvicollis* (Hbn.)
May 30, 1991–Sep. 9, 1989 Count 31

Family LYMANTRIDAE

- 8296 *Dasychira basiflava* (Pack.)
July 5, 1991–Aug. 16, 1990 Count 39
- 8302 *Dasychira obliquata* (G. & R.)
Aug. 9, 1990–Aug. 21, 1989 Count 6
- 8314 *Orgyia definita* Pack.
July 8, 1988–Sep. 14, 1990 Count 5
- 8316 *Orgyia leucostigma* (J.E. Smith)
July 20, 1991–Sep. 10, 1988 Count 9
- 8318 *Lymantria dispar* (L.)
July 5, 1991–Aug. 27, 1992 Count 322

Family NOCTUIDAE

- 8322 *Idia americalis* (Gn.)
May 30, 1991–Sep. 25, 1992 Count 94
- 8323+ *Idia aemula* Hbn.
May 30, 1991–Sep. 21, 1990 Count 66
- 8326 *Idia rotundalis* (Wlk.)
July 5, 1991–Sep. 10, 1992 Count 201
- 8327 *Idia forbesi* (French)
July 4–July 31, 1989 Count 28
- 8329 *Idia diminutis* (B. & McD.)
July 4, 1989–Aug. 27, 1992 Count 135
- 8334 *Idia lubricalis* (Gey.)
July 5–Sep. 13, 1991 Count 30
- 8338 *Phalaenophana pyramusalis* (Wlk.)
June 4, 1989–Aug. 26, 1988 Count 8
- 8340 *Zanclognatha lituralis* (Hbn.)
June 1, 1990–Aug. 19, 1988 Count 5
- 8345 *Zanclognatha laevigata* (Grt.)
July 12, 1991–Sep. 2, 1989 Count 19
- 8348 *Zanclognatha pedipalis* (Gn.)
Aug. 19, 1988 Count 1
- 8349 *Zanclognatha protummalis* (Wlk.)
July 5, 1991–July 31, 1989 Count 7
- 8351 *Zanclognatha cruralis* (Gn.)
June 8, 1990–July 22, 1988 Count 12
- 8352+ *Zanclognatha jachusalis* (Wlk.)
June 20, 1991–Sep. 21, 1990 Count 142
- 8355 *Chytolita morbidalis* (Gn.)
June 1, 1988–July 10, 1992 Count 60
- 8356 *Chytolita petrealis* Grt.
June 15, 1990–Aug. 27, 1992 Count 27
- 8357 *Macrochilo absorptalis* (Wlk.)
July 4, 1989–July 27, 1990 Count 8
- 8357.1 *Macrochilo hypocritalis* Fgn.
July 4–July 17, 1989 Count 3
- 8358 *Macrochilo litophora* (Grt.)
June 27, 1991–Aug. 9, 1990 Count 12
- 8360 *Macrochilo orciferalis* (Wlk.)
June 12–Aug. 27, 1992 Count 3
- 8361 *Macrochilo louisiana* (Fbs.)
July 12, 1991 Count 1

- 8362 *Phalaenostola metonalis* (Wlk.)
June 1, 1988–Sep. 7, 1990 Count 15
- 8363 *Phalaenostola eumelusalis* (Wlk.)
July 20, 1990 Count 1
- 8364 *Phalaenostola larentioides* Grt.
June 29, 1990–Aug. 14, 1989 Count 2
- 8368 *Tetanolita floridana* (Sm.)
July 3–Aug. 7, 1992 Count 2
- 8370 *Bleptina caradrinalis* Gn.
June 20, 1991–July 24, 1989 Count 6
- 8378 *Renia salusalis* (Wlk.)
July 17, 1992 Count 4
- 8379 *Renia factiosalis* (Wlk.)
July 12, 1991–Aug. 27, 1992 Count 29
- 8381 *Renia discoloralis* Gn.
July 19, 1991–Aug. 27, 1992 Count 28
- 8386 *Renia adspersigillus* (Bosc)
June 6, 1991–Aug. 27, 1992 Count 32
- 8387 *Renia sobrialis* (Wlk.)
July 4, 1989–July 24, 1992 Count 10
- 8393 *Lascoria ambigua* Wlk.
June 5, 1992–July 27, 1990 Count 2
- 8397 *Palthis angulalis* (Hbn.)
June 1, 1988–Sep. 13, 1991 Count 10
- 8398 *Palthis asopalalis* (Gn.)
June 26, 1992–Sep. 13, 1991 Count 27
- 8404 *Rivula propinquialis* Gn.
May 30, 1991–Sep. 24, 1988 Count 34
- 8411 *Colobochyla interpuncta* (Grt.)
June 12–July 31, 1989 Count 11
- 8412 *Melanomma auricinctaria* Grt.
June 1, 1990–Sep. 9, 1989 Count 19
- 8421 *Hypenodes fractilinea* (Sm.)
June 5–June 26, 1992 Count 27
- 8426 *Dyspyralis illocata* Warr.
July 12–July 19, 1991 Count 5
- 8427 *Dyspyralis puncticosta* (Sm.)
July 5–July 19, 1991 Count 13
- 8428 *Dyspyralis nigella* (Stkr.)
July 5, 1991–Aug. 14, 1989 Count 63
- 8441 *Bomolocha manalis* (Wlk.)
June 15, 1990–Sep. 13, 1991 Count 18
- 8442 *Bomolocha baltimoralis* (Gn.)
June 12, 1989–Sep. 7, 1990 Count 44
- 8444 *Bomolocha palparia* (Wlk.)
June 1, 1990–Aug. 14, 1989 Count 6
- 8445 *Bomolocha abalienalis* (Wlk.)
Aug. 9–Sep. 7, 1990 Count 3
- 8446 *Bomolocha deceptalis* (Wlk.)
July 19, 1991–July 29, 1988 Count 2
- 8465 *Plathypena scabra* (F.)
June 20–Sep. 21, 1991 Count 16
- 8479 *Spargaloma sexpunctata* Grt.
June 8, 1990–Sep. 6, 1991 Count 10
- 8481 *Phytometra rhodarialis* (Wlk.)
Aug. 14, 1989 Count 1
- 8490 *Pangrapta decoralis* Hbn.
May 30, 1991–Sep. 9, 1989 Count 36

8491	<i>Ledaea perditialis</i> (Wlk.) May 21, 1989–Aug. 27, 1992	Count 113	8857	<i>Catocala ultronii</i> (Hbn.) July 19, 1991–Sep. 25, 1992	Count 15
8499	<i>Metactra discalis</i> (Grt.) July 24–July 31, 1989	Count 2	8858	<i>Catocala crataegi</i> Saund. July 20, 1990–July 22, 1988	Count 3
8514	<i>Scolecocampa liburnia</i> (Gey.) June 20, 1991–Aug. 14, 1989	Count 40	8863	<i>Catocala mira</i> Grt. July 19, 1991–Aug. 27, 1992	Count 27
8555	<i>Scolipteryx libatrix</i> (L.) July 24, 1992	Count 1	8864	<i>Catocala grynea</i> (Cram.) June 27, 1991–Sep. 9, 1989	Count 73
8587	<i>Panopoda rufinargo</i> (Hbn.) June 15–Aug. 5, 1988	Count 18	8865	<i>Catocala praecleara</i> G. & R. July 13–Aug. 24, 1990	Count 10
8588	<i>Panopoda carneicosta</i> Gn. July 10–July 24, 1989	Count 3	8867	<i>Catocala blandula</i> Hulst July 15–July 29, 1988	Count 2
8689	<i>Zale lunata</i> (Drury) July 5, 1991–Sep. 14, 1990	Count 6	8878	<i>Catocala amica</i> (Hbn.) July 22, 1988–Sep. 14, 1990	Count 10
8697	<i>Zale minerea</i> (Gn.) June 1, 1990–July 31, 1989	Count 14	8881	<i>Abrastola urentis</i> Gn. July 12, 1991	Count 1
8716	<i>Zale unilineata</i> (Grt.) June 15, 1988	Count 1	8898	<i>Allagrapha aerea</i> (Hbn.) June 6, 1991–Sep. 14, 1990	Count 22
8717	<i>Zale horrida</i> Hbn. June 4, 1989–July 22, 1988	Count 14	8908	<i>Autographa precatonius</i> (Gn.) June 4, 1989–Sep. 25, 1992	Count 17
8719	<i>Euparthenos nubilis</i> (Hbn.) July 6, 1990	Count 1	8924	<i>Anagrapha falcifera</i> (Kby.) July 12, 1991–Sep. 25, 1992	Count 5
8721	<i>Allotria elonympha</i> (Hbn.) June 1, 1988–Aug. 27, 1992	Count 25	8952	<i>Plusia comtexta</i> Grt. July 19, 1991	Count 1
8727	<i>Parallelia bistriaris</i> Hbn. June 1, 1988–Sep. 13, 1991	Count 41	8956	<i>Marathyssa basalis</i> Wlk. May 28, 1989	Count 1
8738+	<i>Caenurgina crassiuscula</i> (Haw.) July 22, 1988–Aug. 30, 1991	Count 3	8957	<i>Paectes oculatrix</i> (Gn.) June 22, 1988–Aug. 14, 1989	Count 3
8764	<i>Argyrostromis anilis</i> (Drury) July 4, 1989–Aug. 19, 1988	Count 2	8970	<i>Baileya ophiolunica</i> (Gn.) May 21, 1989–July 3, 1992	Count 61
8778	<i>Catocala habilis</i> Grt. Aug. 31–Sep. 14, 1990	Count 3	8971	<i>Baileya dormitans</i> (Gn.) June 1, 1988–June 26, 1992	Count 11
8781	<i>Catocala Judith</i> Stkr. Sep. 2, 1989	Count 1	8972	<i>Baileya levitans</i> (Sm.) June 22, 1988–Aug. 7, 1989	Count 6
8785	<i>Catocala residua</i> Grt. Aug. 31–Sep. 14, 1990	Count 3	8973	<i>Baileya anstralis</i> (Grt.) June 1, 1990	Count 1
8788	<i>Catocala relecta</i> Grt. Aug. 19, 1988–Sep. 9, 1989	Count 7	8983	<i>Meganola minuscula</i> (Zell.) May 18, 1988–Aug. 7, 1989	Count 111
8792	<i>Catocala vidua</i> (J.E. Smith) Aug. 2, 1991–Sep. 14, 1990	Count 3	8983.1	<i>Meganola phylla</i> (Dyar) June 12, 1989–Aug. 19, 1988	Count 13
8795	<i>Catocala palaeogama</i> Gn. Aug. 24, 1990–Aug. 27, 1992	Count 2	8983.2	<i>Meganola spodia</i> Franc. June 22, 1990–July 31, 1989	Count 17
8797	<i>Catocala subnata</i> Grt. Aug. 21, 1989	Count 1	9030	<i>Ozarba aerea</i> (Grt.) July 5, 1991	Count 1
8801	<i>Catocala ilia</i> (Cram.) July 5, 1991–Sep. 25, 1992	Count 13	9037	<i>Hyperstrotia pervertens</i> (B. & McD.) May 30, 1991–July 27, 1990	Count 30
8802	<i>Catocala cerogama</i> Gn. Aug. 26, 1988–Aug. 27, 1992	Count 2	9038	<i>Hyperstrotia villificans</i> (B. & McD.) June 19, 1989–July 12, 1991	Count 16
8803	<i>Catocala relictus</i> Wlk. Aug. 26, 1988	Count 1	9040	<i>Hyperstrotia secta</i> (Grt.) July 10, 1989–Aug. 7, 1992	Count 11
8805	<i>Catocala unijuga</i> Wlk. Aug. 26, 1988–Sep. 9, 1989	Count 2	9044	<i>Thioptera nigrofimbria</i> (Gn.) July 12, 1991	Count 1
8832	<i>Catocala cara</i> Gn. Aug. 19, 1988–Sep. 21, 1990	Count 3	9046	<i>Lithacodia bellicula</i> Hbn. June 1, 1990–July 29, 1988	Count 5
8833	<i>Catocala concumbens</i> Wlk. Aug. 19, 1988	Count 1	9047	<i>Lithacodia muscosula</i> (Gn.) May 30–Aug. 30, 1991	Count 265
8851	<i>Catocala coccinata</i> Grt. July 13–Aug. 16, 1990	Count 6	9048	<i>Lithacodia albidula</i> (Gn.) June 27–Aug. 2, 1991	Count 8

- 9053 *Pseudostrotia carneola* (Gn.)
May 30, 1991–Aug. 21, 1989 Count 71
- 9055.1 *Maliathya synochitis* (G. & R.)
June 15, 1990–July 29, 1988 Count 19
- 9056 *Homophoberia cristata* Morr.
July 3, 1992–Aug. 21, 1989 Count 6
- 9057 *Homophoberia apicosa* (Haw.)
May 30, 1991–Aug. 24, 1990 Count 78
- 9062 *Cerna cerintha* (Tr.)
June 15–July 15, 1988 Count 19
- 9065 *Leuconycta dipteroides* (Gn.)
May 30–Aug. 2, 1991 Count 16
- 9066 *Leuconycta lepidula* (Grt.)
June 1–Aug. 19, 1988 Count 8
- 9090 *Tarachidia candefacta* (Hbn.)
June 15, 1988–Sep. 6, 1991 Count 6
- 9095 *Tarachidia erastrioides* (Gn.)
June 15, 1988–Sep. 6, 1991 Count 12
- 9185 *Colocasia propinquilinea* (Grt.)
May 30–July 12, 1991 Count 52
- 9193 *Raphia frater* Grt.
May 30–Aug. 2, 1991 Count 16
- 9200 *Acronicta americana* (Harr.)
May 30, 1991–July 27, 1990 Count 12
- 9203 *Acronicta dactylina* Grt.
June 22, 1988–July 19, 1991 Count 3
- 9227 *Acronicta laetifica* Sm.
June 13, 1991–July 29, 1988 Count 3
- 9229 *Acronicta hasta* Gn.
May 28–Aug. 7, 1989 Count 9
- 9235 *Acronicta spinigera* Gn.
May 30, 1991–Aug. 14, 1989 Count 36
- 9237 *Acronicta interrupta* Gn.
July 24–Aug. 21, 1989 Count 3
- 9238 *Acronicta lobeliae* Gn.
June 8, 1990–Aug. 14, 1989 Count 2
- 9242 *Acronicta exilis* Grt.
June 15, 1988–Aug. 7, 1989 Count 7
- 9243 *Acronicta ovata* Grt.
May 30, 1991–Aug. 5, 1988 Count 59
- 9244 *Acronicta modica* Wlk.
June 12, 1989–Aug. 5, 1988 Count 19
- 9245+ *Acronicta haesitata* (Grt.)
May 30–Aug. 2, 1991 Count 224
- 9251 *Acronicta retardata* (Wlk.)
June 22, 1988–Aug. 16, 1990 Count 3
- 9261 *Acronicta impressa* Wlk.
July 5, 1991–Aug. 21, 1989 Count 12
- 9272 *Acronicta oblinta* (J.E. Smith)
June 15, 1988–Aug. 21, 1989 Count 3
- 9285 *Polygrammate hebraeicum* Hbn.
May 30, 1991–July 29, 1988 Count 101
- 9286 *Harrisimemna trisignata* (Wlk.)
July 24, 1989 Count 1
- 9301 *Eudryas grata* (F.)
May 30, 1991–July 31, 1989 Count 12
- 9328 *Apamea nigrior* (Sm.)
June 29, 1988–July 6, 1990 Count 2
- 9332 *Apamea vulgaris* (G. & R.)
June 27, 1991 Count 1
- 9348 *Apamea amputatrix* (Fitch)
July 24–Aug. 27, 1992 Count 2
- 9364 *Apamea sordens* (Hufn.)
June 26, 1992–Aug. 2, 1991 Count 2
- 9373 *Apamea helva* (Grt.)
Aug. 14, 1989 Count 1
- 9404 *Oligia modica* (Gn.)
July 17, 1989–Aug. 30, 1991 Count 5
- 9406 *Oligia fragilinea* (Grt.)
July 20, 1990–Aug. 16, 1991 Count 3
- 9419 *Oligia mactata* (Gn.)
Sep. 14, 1990 Count 1
- 9427 *Meropon diversicolor* (Morr.)
Aug. 31, 1990–Sep. 13, 1991 Count 7
- 9449 *Archana oblonga* (Grt.)
Aug. 19, 1988 Count 1
- 9454 *Amphipoea velata* (Wlk.)
June 20, 1991 Count 1
- 9457+ *Amphipoea americana* (Speyer)
July 27, 1990–Aug. 7, 1992 Count 2
- 9463 *Parapamea buffaloensis* (Grt.)
Aug. 26, 1988–Sep. 9, 1989 Count 2
- 9471 *Papaipema activorens* Hamp.
Sep. 10, 1988 Count 1
- 9483 *Papaipema inquaesita* (G. & R.)
Aug. 23, 1991–Sep. 25, 1992 Count 11
- 9485 *Papaipema baptisiae* (Bird)
Sep. 9, 1989–Sep. 14, 1990 Count 4
- 9486 *Papaipema birdi* (Dyar)
Aug. 21, 1989–Sep. 13, 1991 Count 4
- 9490 *Papaipema nepheleptena* (Dyar)
Sep. 21, 1990 Count 1
- 9503 *Papaipema rigida* (Grt.)
Sep. 9, 1989 Count 1
- 9505 *Papaipema cerussata* (Grt.)
Sep. 9, 1989–Sep. 25, 1992 Count 5
- 9509 *Papaipema unimoda* (Sm.)
Sep. 14–Sep. 21, 1990 Count 2
- 9520 *Achatodes zeae* (Harr.)
June 20, 1991–Aug. 5, 1988 Count 3
- 9523 *Bellura gortynoides* Wlk.
July 12, 1991–Aug. 14, 1989 Count 2
- 9525 *Bellura obliqua* (Wlk.)
June 1, 1990–June 4, 1989 Count 2
- 9526 *Bellura densa* (Wlk.)
July 31, 1989 Count 1
- 9545 *Euplexia benesimilis* McD.
May 30, 1991–Aug. 9, 1990 Count 45
- 9546 *Phlogophora iris* Gn.
June 1–June 15, 1988 Count 3
- 9547 *Phlogophora periculosa* Gn.
July 3–Sep. 10, 1992 Count 10
- 9549 *Enargia decolor* (Wlk.)
July 19, 1991 Count 1
- 9550 *Enargia infumata* (Grt.)
July 17, 1992 Count 1

9551	<i>Euargia mephisto</i> Franc. June 22, 1990–July 3, 1992	Count 5	9961	<i>Anathix ralla</i> (G. & R.) Aug. 19, 1988–Sep. 25, 1992	Count 17
9555	<i>Ipinorpha pleonectusa</i> Grt. May 19, 1991–Sep. 9, 1989	Count 13	9962	<i>Anathix puta</i> (G. & R.) Sep. 2, 1989	Count 1
9556	<i>Chytonix palliatricula</i> (Gn.) June 1, 1988–Aug. 3, 1990	Count 83	9989	<i>Stryna privata</i> (Wlk.) Sep. 9, 1989	Count 1
9560	<i>Dypterygia rozmani</i> Berio June 12, 1989	Count 1	10033	<i>Catabena lineolata</i> Wlk. July 4, 1989	Count 1
9578	<i>Hyppa xylinoidea</i> (Gn.) May 30, 1991–Aug. 27, 1992	Count 16	10194	<i>Cucullia lucifuga</i> (D. & S.) Aug. 16, 1990	Count 1
9582	<i>Nedra ramosula</i> (Gn.) July 19, 1991–Sep. 21, 1990	Count 2	10200	<i>Cucullia asteroides</i> Gn. Aug. 19, 1988	Count 1
9618	<i>Phosphila turbulenta</i> Hbn. June 20, 1991–July 13, 1990	Count 2	10202	<i>Cucullia convexipennis</i> G. & R. July 12, 1991	Count 1
9619	<i>Phosphila miseloides</i> (Gn.) June 26, 1992–July 13, 1990	Count 3	10275	<i>Polia nimbosea</i> (Gn.) June 22, 1990–Aug. 27, 1992	Count 2
9631	<i>Callopietria mollissima</i> (Gn.) May 30–Aug. 16, 1991	Count 16	10276	<i>Polia inbrifera</i> (Gn.) June 13, 1991–June 29, 1988	Count 8
9638	<i>Amphipyra pyramidoides</i> Gn. July 22, 1988–Sep. 25, 1992	Count 128	10288+	<i>Polia detracta</i> (Wlk.) May 30–Aug. 23, 1991	Count 649
9647	<i>Athetis miranda</i> (Grt.) July 3, 1992–Aug. 19, 1988	Count 2	10292	<i>Melanarcha adjuncta</i> (Gn.) Aug. 9, 1990–Aug. 19, 1988	Count 3
9650	<i>Anorthodes tarda</i> (Gn.) June 5–Sep. 25, 1992	Count 16	10299	<i>Lacanobia subjuncta</i> (G. & R.) June 1, 1990–July 19, 1991	Count 2
9662	<i>Balsa malana</i> (Fitch) June 15–Aug. 16, 1990	Count 8	10300	<i>Spiramater grandis</i> (Gn.) June 8–June 15, 1988	Count 3
9663	<i>Balsa tristrigella</i> (Wlk.) May 30, 1991–July 10, 1989	Count 103	10301	<i>Spiramater lutra</i> (Gn.) June 15, 1988	Count 1
9664	<i>Balsa labecula</i> (Grt.) June 15–July 29, 1988	Count 17	10368	<i>Lacinipolia meditata</i> (Grt.) Aug. 19, 1988	Count 2
9678	<i>Elaphria versicolor</i> (Grt.) June 26, 1989	Count 1	10397	<i>Lacinipolia renigera</i> (Steph.) June 12–Sep. 9, 1989	Count 45
9681	<i>Elaphria festivoides</i> (Gn.) May 30, 1991–July 8, 1988	Count 6	10405	<i>Lacinipolia lorea</i> (Gn.) June 6, 1991–July 10, 1989	Count 38
9688	<i>Galgula partita</i> Gn. June 10, 1992–Aug. 26, 1988	Count 5	10436	<i>Aletia oxygala</i> (Grt.) May 30–Aug. 30, 1991	Count 14
9689	<i>Perigea xanthoides</i> Gn. May 30, 1991–Sep. 9, 1989	Count 67	10438	<i>Pseudaletia unipuncta</i> (Haw.) May 18–Sep. 10, 1988	Count 34
9690	<i>Platysenta videns</i> (Gn.) June 15–June 29, 1988	Count 5	10444+	<i>Leucania phragmatidicola</i> Gn. July 3, 1992	Count 2
9696	<i>Platysenta vecors</i> (Gn.) June 8, 1990–Aug. 7, 1992	Count 5	10446+	<i>Leucania multilinea</i> Wlk. May 30, 1991–Aug. 24, 1990	Count 8
9720	<i>Ogdoconta cinereola</i> (Gn.) May 30, 1991–Sep. 7, 1990	Count 74	10447	<i>Leucania connoides</i> Gn. Sep. 25, 1992	Count 1
9725	<i>Stiriodes obtusa</i> (H.-S.) June 8, 1990	Count 1	10461+	<i>Leucania nrsula</i> (Fbs.) June 12, 1992–Sep. 2, 1989	Count 22
9815	<i>Cosmia calami</i> (Harv.) July 10, 1989–Aug. 7, 1992	Count 48	10495+	<i>Orthosia hibisci</i> (Gn.) July 10, 1989	Count 1
9818	<i>Amolita fessa</i> Grt. June 20, 1991–July 17, 1992	Count 15	10501	<i>Crocigrapta normani</i> (Grt.) May 18, 1988–June 12, 1992	Count 4
9878	<i>Lithomoia gernana</i> (Morr.) Sep. 10, 1988	Count 1	10521	<i>Morrisonia confusa</i> (Hbn.) May 18, 1988–June 12, 1992	Count 7
9888	<i>Lithophane inominata</i> (Sm.) Sep. 14, 1990	Count 1	10521.1	<i>Morrisonia latex</i> (Gn.) June 1–June 29, 1988	Count 13
9889	<i>Lithophane petulca</i> Grt. Sep. 21, 1990	Count 1	10524	<i>Nephelodes minians</i> Gn. Aug. 23, 1991–Sep. 25, 1992	Count 83
9957	<i>Sumira bicolorago</i> (Gn.) Sep. 21, 1990–Sep. 25, 1992	Count 2	10532	<i>Homorthodes furfurata</i> (Grt.) June 20, 1991–July 15, 1988	Count 8

10563	<i>Protorthodes oviduca</i> (Gn.) May 28, 1989.	Count 1	10942.1+	<i>Xestia dolosa</i> Franc. May 30, 1991–Sep. 25, 1992.	Count 225
10578	<i>Pseudorthodes vecors</i> (Gn.) June 1, 1988–Aug. 27, 1992.	Count 41	10943	<i>Xestia normaniana</i> (Grt.) Aug. 7, 1992–Sep. 13, 1991.	Count 61
10585	<i>Orthodes crenulata</i> (Butler) June 1–Aug. 19, 1988.	Count 9	10944	<i>Xestia smithii</i> (Snell.) Aug. 19, 1988–Sep. 25, 1992.	Count 53
10587	<i>Orthodes cynica</i> Gn. May 30, 1991–Sep. 25, 1992.	Count 175	10950+	<i>Xestia bicarnea</i> (Gn.) July 29–Sep. 10, 1988.	Count 84
10627	<i>Tricholita signata</i> (Wlk.) July 10, 1992–Sep. 6, 1991.	Count 11	10954	<i>Xestia bugrai</i> Kocak Sep. 14, 1990.	Count 1
10663	<i>Agrotis ipsilon</i> (Hufn.) May 28, 1989–Sep. 25, 1992.	Count 24	10998	<i>Choeophora fungorum</i> G. & R. Sep. 10, 1988.	Count 1
10674+	<i>Feltia subgothica</i> (Haw.) July 19, 1991–Sep. 10, 1988.	Count 16	11000	<i>Anaplectoides prasina</i> (D. & S.) June 27, 1991.	Count 1
10676	<i>Feltia herilis</i> (Grt.) July 31, 1989–Sep. 25, 1992.	Count 51	11006	<i>Protolampra brunneicollis</i> (Grt.) June 15, 1990–Sep. 2, 1989.	Count 67
10891	<i>Ochropleura plecta</i> (L.) May 18, 1988–Sep. 13, 1991.	Count 160	11010	<i>Heptagrotis phyllophora</i> (Grt.) June 29, 1988–July 3, 1992.	Count 6
10903+	<i>Euagrotis illapsa</i> (Wlk.) Aug. 2, 1991–Sep. 10, 1988.	Count 4	11029+	<i>Abagrotis alternata</i> (Grt.) July 5, 1991–Sep. 25, 1992.	Count 28
10915	<i>Peridroma saucia</i> (Hbn.) June 29, 1988.	Count 2	11149	<i>Schinia trifascia</i> Hbn. July 27, 1990–July 29, 1988.	Count 2
10929	<i>Eurois occulta</i> (L.) Aug. 3, 1990–Aug. 21, 1992.	Count 2			

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CHECKLIST OF THE MOTHS OF LAKE CARDINAL SWAMP, ASHTABULA COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Lake Cardinal Swamp on Lake Cardinal Estates in Ashtabula County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988–1992) and includes 21,842 specimens representing 532 species. The study continued through 1996, but only data for 1988–1992 are included here. The checklist is a historical record of the species that were present in 1988–1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after nine years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988–1992 is 6.87 and the Shannon-Wiener Evenness Index is 0.76. Two hundred thirteen of the 532 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. The less abundant species at Lake Cardinal Swamp are not less likely to be widespread. Five species of owlet moths that were collected at Lake Cardinal Swamp are of special interest in Ohio and one species has been listed as endangered. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Introduction

The objective of this study was to document the population changes of native moths for ten years at several sites within the drainage basin of the Grand River in Trumbull, Ashtabula, and Lake Counties, Ohio, during gypsy moth invasion and control. This is the second in a series of six checklists that tabulate the moths collected at each site during 1988–1992.

Over this same period, the population of the gypsy moth increased in the entire drainage basin. Pheromone trap catches of male gypsy moths increased at Lake Cardinal Swamp from $44 \pm 14(2)$ per trap in 1987 [mean \pm standard error (number of traps)], to $20 \pm 5(4)$ in 1988, $88 \pm 24(4)$ in 1989, $48 \pm 11(4)$ in 1990, and $121 \pm 23(4)$ in 1991. Pheromone trapping was discontinued after 1991. Ultraviolet-light-trap catches of male gypsy moths also increased, from 7 in 1988, to 41 in 1989, 36 in 1990, 37 in 1991, and 61 in 1992, but noticeable defoliation was not observed at Lake Cardinal Swamp except for isolated trees.

The overall study provides baseline data on pre-outbreak moth diversity, as well as data on the impact of gypsy moth control agents.

Description of the Surveillance Site at Lake Cardinal Swamp

The Lake Cardinal Estates are composed of 294 ha of lake, forest, and residential allotments located in Rome Township, Ashtabula County, and bordered on the south by U.S. Route 6 (Figure 1). They are situated on swampy glacial lake plain with fine-grained lacustrine silt and clay soils (White and Totten, 1979, p. 7, Pl. 1) overlain by rich organic muck. The Estates are part of a much larger forested area of approximately 1800 ha that extends 6 km north, and 3 km east (Anonymous, 1995).

The light trap at Lake Cardinal Swamp was located within The Estates at latitude $41^{\circ} 36' 39''$ N and longitude $80^{\circ} 53' 32''$ W (U.S. Geological Survey Windsor and East Trumbull, Ohio, 7.5-minute quadrangle topographic maps; Figure 1). The Swamp is located in the south-central part of The Estates and covers an area of 54 ha.

The Lake Cardinal Estates are approximately 25 km east/northeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

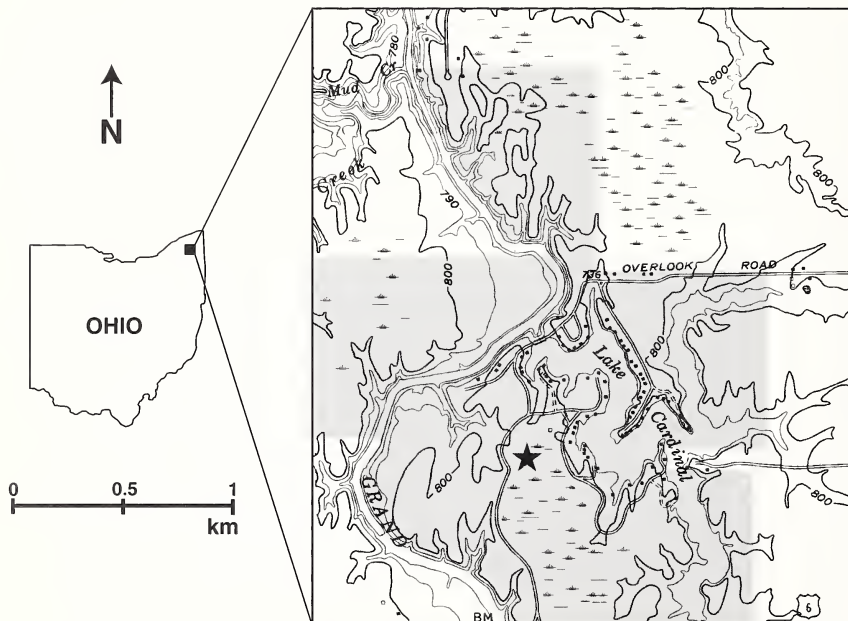


Figure 1. Map of the study area (adapted from the U.S. Geological Survey Windsor and East Trumbull, Ohio, 7.5-minute quadrangle topographic maps). Shaded area delineates Lake Cardinal Estates; star indicates position of surveillance trap within the Swamp.

Table 1. The importance values for trees at the surveillance site at Lake Cardinal Swamp. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Tree Species		Canopy Understory	
Beech, American	<i>Fagus grandifolia</i> Ehrh.	76	164
Maple, red	<i>Acer rubrum</i> L.	74	18
Oak, northern red	<i>Quercus rubra</i> L.	40	0
Cherry, black	<i>Prunus serotina</i> Ehrh.	39	19
Oak, white	<i>Quercus alba</i> L.	38	0
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees	11	0
Maple, silver	<i>Acer saccharinum</i> L.	8	0
Tupelo, black	<i>Nyssa sylvatica</i> Marsh.	7	57
Magnolia, cucumber	<i>Magnolia acuminata</i> (L.) L.	7	0
Shadbush	<i>Amelanchier arborea</i> (Michx.) F. Fern.	0	9
Ash	<i>Fraxinus</i> spp.	0	8
Birch, yellow	<i>Betula alleghaniensis</i> Britt.	0	8
Hop Hornbeam, eastern	<i>Ostrya virginiana</i> (Mill.) K. Koch	0	8
Witch-hazel	<i>Hamamelis virginiana</i> L.	0	8

The composition of the canopy and understory was evaluated for the 2500 m² of forest centered on the surveillance trap (point-quarter technique, nine points; Cottam and Curtis, 1956; Cox, 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90 m in the Lake Cardinal Swamp. The importance values for the trees at the surveillance site at Lake Cardinal Swamp are given in Table 1.

The herbaceous plants and small shrubs in Lake Cardinal Swamp included: crippled crane-fly orchid *Tipularia discolor* (Pursh) Nutt.; sedges *Carex seorsa* Howe and *Carex folliculata* L.; bur-reed *Sparganium americanum* Nutt.; hedge-hyssop *Gratiola neglecta* Torr.; creeping wintergreen *Gaultheria procumbens* L.; goldthread *Coptis trifolia* (L.) Salisb. ssp. *groenlandica* (Oeder) Hulten.; *Dalibarda repens* L.; ferns *Osmunda cinnamomea* L. and *Osmunda regalis* L.; blue verberna *Verberna hastata* L.; rhododendrons *Rhododendron periclymenoides* (Michx.) Shinners and *Rhododendron prinophyllum* (Small) Millais; and blueberries *Vaccinium corymbosum* L. and *Vaccinium myrtilloides* var. Michx. (James K. Bissell, 1998, personal communication; author citations according to Kartesz, 1994). These species were selected from a longer list of Lake Cardinal species on deposit in the Herbarium at the Cleveland Museum of Natural History. The selected species are indicative of the uniqueness of the habitat at Lake Cardinal.

Surveillance Techniques

One Elliscope®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, from late

May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were computerized. All the specimens collected are deposited in the Insect Collection of The Cleveland Museum of Natural History.

Results and Discussion

A total of 21,842 specimens representing 532 species were collected in 1988–1992 (Appendix). Species were identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al. (1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodges et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 35 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1988 to 1996, is shown in Figure 2. In 1988, 341 species were collected and in 1996, after nine years, the total had reached 624 (1993–1996 not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Lake Cardinal Swamp and five years would have been a minimum. The species accumulation curve was still rising after nine years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: fall, winter, and early spring moths are missing because collecting was not begun until the end of May and collecting ended in September. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

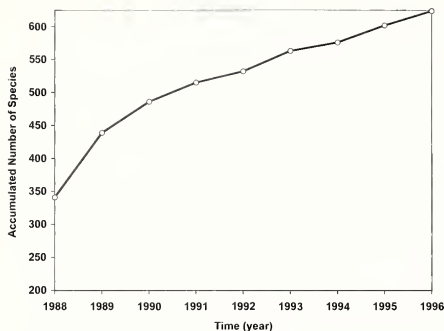


Figure 2. Plot of the annual accumulation of species collected at Lake Cardinal Swamp on Lake Cardinal Estates, 1988–1996.

Relative abundances of the 532 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The

Shannon-Wiener Diversity Index is 6.87 and the Shannon-Wiener Evenness Index is 0.76.

Seventeen percent of the total count was composed of lesser maple spanworm moth *Itame pustularia* (6273). The next most abundant species was sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants. Following, in order of decreasing abundance, were: rotund idia *Idia rotundalis* (8326) whose larva feeds on dead coral fungus and dead leaves; banded tussock moth *Halysidota tessellaris* (8203+) whose larva feeds on many deciduous trees; disparaged arches *Polia detrecta* (10288+) whose larva feeds on clover, blueberries, oaks, etc.; oak leafroller moth *Argyrotaenia alisellana* (3624) whose larva feeds on oaks; pyraustinid *Crociodophora serratissimalis* (4944) whose larva feeds on rice cutgrass; large mossy lithacodia *Lithacodia muscosula* (9047) whose larva feeds on grasses in swamps; agreeable tiger moth *Spilosoma congrua* (8134) whose larva feeds on various herbaceous plants; and orange-spotted idia *Idia diminuendus* (8329) whose larval host is unrecorded.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 213 Lake Cardinal Swamp species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988, 1990). Three explanations have been proposed (Krebs, 1994). First, the

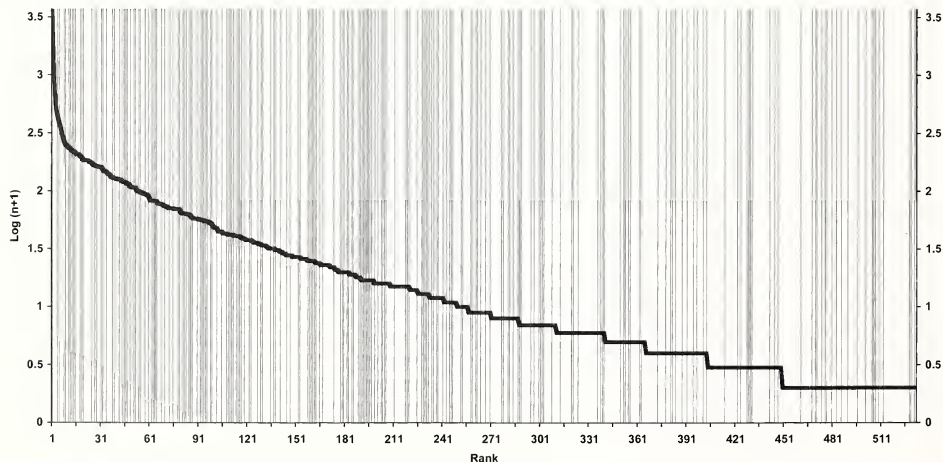


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Lake Cardinal Swamp on Lake Cardinal Estates, 1988–1992.

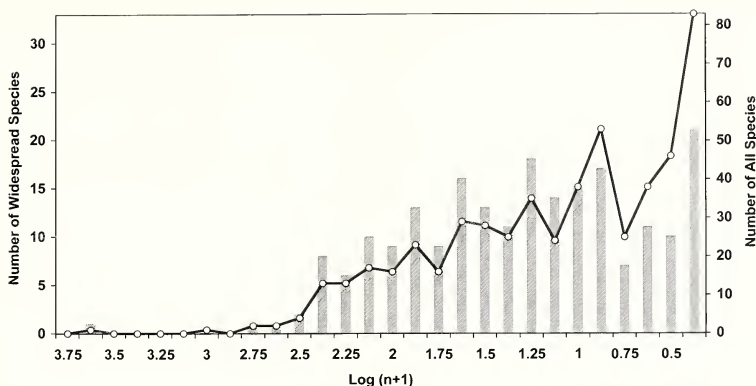


Figure 4. Correspondence between the total number of Lake Cardinal Swamp species in an abundance interval (line, scale at right) and the number of widespread Lake Cardinal Swamp species in the same abundance interval (bar, scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not exist, when abundance is viewed from the perspective of abundance at Lake Cardinal Swamp. Of the 213 Lake Cardinal species which are widespread in northeast Ohio, 85 had total counts of 10 or fewer at Lake Cardinal.

Overall, there is a close correspondence between the number of widespread species in an abundance interval and the total number of species (Figure 4).

One species of owl moth collected at Lake Cardinal Swamp, graceful underwing *Catocala gracilis* (8847), is listed as endangered in Rings et al. (1992). Its larva feeds on blueberries and two species of blueberry have been recorded from Lake Cardinal Estates: *Vaccinium corymbosum* L. and *V. myrtilloides* var. Michx. Five species of owl moths collected at Lake Cardinal Swamp are listed as being of special interest in Rings et al. (1992): gray-banded zale *Zale squamularis* (8700) whose larva feeds on pines; formosa looper moth *Chrysanympha formosa* (8904) whose larva feeds on blueberry and dwarf huckleberry; airy apamea *Apamea vultuosa* (9341) whose larva feeds on grasses; puta sawfly *Anathix puta* (9962) whose larva feeds on quaking aspen; and scurfy quaker *Homorthodes fufurata* (10532) whose larva feeds on maples.

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Appendix. Checklist of the species collected at Lake Cardinal Swamp on Lake Cardinal Estates, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection, and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family HEPIALIDAE

- 20 *Sthenopis quadriguttatus* (Grt.)
July 5, 1991..... Count 1

Family TINEIDAE

- 372+ *Acrolophus plumifrontella* (Clem.)
July 10, 1992..... Count 2

Family OECOPHORIDAE

- 882 *Agonopterix robinella* (Pack.)
June 1–Aug. 5, 1988..... Count 20
- 951 *Machimia tentoriferella* Clem.
Sep. 24, 1988..... Count 1
- 957 *Psilocorsis reflexella* Clem.
June 1, 1988–Aug. 9, 1990..... Count 147
- 1014+ *Antaeotricha leucillana* (Zell.)
May 18, 1988–Aug. 24, 1990..... Count 165
- 1046 *Callima argenticinctella* Clem.
July 24, 1989..... Count 1

Family GELECHIIDAE

- 2295 *Trichotapha flavocostella* (Clem.)
July 4, 1989–Aug. 9, 1990..... Count 4

Family YPONOMEUTIDAE

- 2401 *Atteva punctella* (Cram.)
July 12, 1991–Sep. 7, 1990..... Count 6
- 2420 *Yponomeuta multipunctella* Clem.
June 20, 1991–July 24, 1992..... Count 126

Family SESIIDAE

- 2554 *Synanthedon acerni* (Clem.)
June 22, 1988–July 10, 1992..... Count 3

Family TORTRICIDAE

- 2784 *Olethreutes footiana* (Fern.)
Aug. 21, 1989..... Count 1
- 2863 *Hedya chionosema* (Zell.)
Aug. 21, 1989..... Count 1
- 3116 *Encosma dorsisignatana* (Clem.)
Sep. 9, 1989..... Count 1
- 3186 *Epiblema scudderiana* (Clem.)
June 1, 1988..... Count 1
- 3361 *Ancylis semiovana* (Zell.)
June 1–June 8, 1988..... Count 69
- 3494 *Melissopus latiferreanus* (Wlsm.)
July 31–Aug. 14, 1989..... Count 9
- 3503 *Croesia semipurpurana* (Kft.)
June 26, 1989..... Count 4
- 3504 *Croesia curvalana* (Kft.)
June 19–July 10, 1989..... Count 8

- 3594 *Pandemis limitata* (Rob.)
June 8, 1990–Aug. 27, 1992..... Count 16
- 3597 *Argyrotaenia velutinana* (Wlk.)
July 3, 1992..... Count 1
- 3623 *Argyrotaenia quercifoliana* (Fitch)
June 6, 1991–Aug. 21, 1992..... Count 168
- 3624 *Argyrotaenia alisellana* (Rob.)
June 6, 1991–July 3, 1992..... Count 350
- 3625 *Argyrotaenia mariana* (Fern.)
June 1, 1988..... Count 1
- 3632 *Choristoneura fractivittana* (Clem.)
June 1–Aug. 26, 1988..... Count 182
- 3633 *Choristoneura parallela* (Rob.)
June 22–Sep. 7, 1990..... Count 12
- 3635 *Choristoneura rosaceana* (Harr.)
June 8–Sep. 14, 1990..... Count 92
- 3648 *Archips argyrosipila* (Wlk.)
June 8, 1990–July 10, 1989..... Count 9
- 3658 *Archips purpurana* (Clem.)
July 24, 1989..... Count 1
- 3686 *Clepsis melaleucana* (Wlk.)
June 1, 1988–June 26, 1989..... Count 42
- 3695 *Sparganothis sulfureana* (Clem.)
June 8, 1990–June 15, 1988..... Count 2
- 3720 *Sparganothis reticulatana* (Clem.)
Aug. 21–Sep. 9, 1989..... Count 2
- 3725 *Sparganothis pettitana* (Rob.)
June 22, 1988–Sep. 9, 1989..... Count 10
- 3748 *Amorbia humerosana* Clem.
June 1–June 15, 1988..... Count 3

Family LIMACODIDAE

- 4652 *Tortricidia testacea* Pack.
June 1, 1988–June 26, 1992..... Count 30
- 4654 *Tortricidia flexuosa* (Grt.)
June 20, 1991–Aug. 16, 1990..... Count 161
- 4659 *Packardia geminata* (Pack.)
June 5–July 3, 1992..... Count 15
- 4661 *Packardia elegans* (Pack.)
June 5, 1992–July 10, 1992..... Count 26
- 4665 *Lithacodes fasciola* (H.-S.)
June 15, 1988–Aug. 7, 1992..... Count 25
- 4667 *Apoda y-inversum* (Pack.)
June 22–July 20, 1990..... Count 12
- 4669 *Apoda biguttata* (Pack.)
June 15, 1988–July 24, 1992..... Count 22
- 4671 *Prolimacodes badia* (Hbn.)
July 5, 1991–July 24, 1989..... Count 6
- 4681 *Isa textula* (H.-S.)
June 22, 1990–July 10, 1992..... Count 3

- 4685 *Adoneta spinuloides* (H.-S.)
June 20, 1991–July 10, 1989 Count 5
- 4697 *Euclea delphinii* (Bdv.)
June 8, 1990–July 22, 1988 Count 16

Family CRAMBIDAE

- 4703 *Gesneria centuriella* (D. & S.)
June 1–Aug. 5, 1988 Count 57
- 4748 *Munroessa icciusalis* (Wlk.)
June 1, 1988–Aug. 30, 1991 Count 162
- 4749 *Munroessa faulalis* (Wlk.)
June 20, 1991 Count 3
- 4751 *Munroessa gyralis* (Hulst)
June 8, 1990–Sep. 9, 1989 Count 56
- 4755 *Synclita oblitteralis* (Wlk.)
July 29, 1988–Aug. 14, 1989 Count 3
- 4794 *Eustixia pupula* Hbn.
July 8, 1988 Count 1
- 4889 *Dicymolomia julianalis* (Wlk.)
July 3, 1992–Sep. 9, 1989 Count 13
- 4897 *Evergestis pallidata* (Hufn.)
June 1, 1990–Sep. 10, 1992 Count 21
- 4936 *Saurobotys futilalis* (Led.)
June 5, 1992–Aug. 30, 1991 Count 6
- 4937 *Nascia acutella* (Wlk.)
June 8, 1990–Aug. 5, 1988 Count 6
- 4944 *Crocidophora serratissimalis* Zell.
June 15, 1988–Sep. 9, 1989 Count 309
- 4945 *Crocidophora tubercularis* Led.
June 20, 1991–July 29, 1988 Count 35
- 4949 *Ostrinia nubilalis* (Hbn.)
June 1, 1988–Sep. 13, 1991 Count 73
- 4950 *Fumibotys fumalis* (Gn.)
July 12, 1991–Sep. 4, 1992 Count 30
- 4951 *Perispasta caeculalis* Zell.
July 12, 1991–Aug. 9, 1990 Count 4
- 4953a *Phlyctaenia coronata tertialis* (Gn.)
July 12–Aug. 2, 1991 Count 4
- 4962 *Hahncappsa marculenta* (G. & R.)
June 1–June 22, 1988 Count 4
- 4975 *Achyra rantalis* (Gn.)
Aug. 21, 1989 Count 5
- 4980 *Helvibotys helvialis* (Wlk.)
June 12, 1989 Count 6
- 5040 *Pyrausta bicoloralis* (Gn.)
June 8–Sep. 14, 1990 Count 69
- 5071 *Pyrausta acronialis* (Wlk.)
June 6, 1991–Sep. 24, 1988 Count 30
- 5079 *Udea rubigalis* (Gn.)
June 1, 1988–Sep. 14, 1990 Count 100
- 5142 *Diacme elealis* (Wlk.)
Apr. 23, 1989–Aug. 7, 1992 Count 31
- 5156 *Nomophila nearctica* Mun.
June 5, 1992–Sep. 13, 1991 Count 2
- 5159 *Desmia funeralis* (Hbn.)
June 15, 1988–Sep. 9, 1989 Count 24
- 5160 *Desmia maculalis* Westwood
July 12, 1991 Count 7

- 5182 *Blepharomastix ranalis* (Gn.)
June 29, 1988 Count 1
- 5226 *Palpita magniferalis* (Wlk.)
June 1–Aug. 3, 1990 Count 44
- 5228 *Polygrammodes flavidalis* (Gn.)
June 15, 1988–Aug. 21, 1989 Count 9
- 5241 *Pantographa limata* (G. & R.)
July 5, 1991–Aug. 19, 1988 Count 24
- 5272 *Herpetogramma bipunctalis* (F.)
June 15, 1988–Aug. 14, 1989 Count 26
- 5275 *Herpetogramma pertextalis* (Led.)
June 22, 1988–Aug. 14, 1989 Count 26
- 5280 *Herpetogramma aeglealis* (Wlk.)
July 5–Aug. 2, 1991 Count 18
- 5281 *Pilocrocis ramentalis* Led.
June 12, 1991–July 22, 1988 Count 4
- 5362+ *Crambus agitatellus* Clem.
June 5, 1992–Sep. 10, 1988 Count 948
- 5392 *Arequipa turbatella* Wlk.
June 20, 1991–July 17, 1992 Count 4
- 5403 *Agriphila vulgivagella* (Clem.)
Sep. 10, 1992 Count 3
- 5464 *Urola nivalis* (Drury)
June 20–Aug. 30, 1991 Count 37
- 5465 *Vaxi auratella* (Clem.)
July 10, 1989–Aug. 3, 1990 Count 14
- 5466 *Vaxi critica* (Fbs.)
July 5, 1991 Count 1

Family PYRALIDAE

- 5518 *Aglossa cuprina* Zell.
June 15, 1990–Aug. 27, 1992 Count 206
- 5524 *Hypsopygia costalis* (F.)
June 29, 1990–Aug. 19, 1988 Count 5
- 5532 *Herculia infimbrialis* Dyar
July 10, 1989–Aug. 16, 1990 Count 5
- 5533 *Herculia olinalis* (Gn.)
June 22, 1988–Aug. 27, 1992 Count 8
- 5552 *Galasa nigrinodis* (Zell.)
July 5, 1991 Count 1
- 5556 *Tosale oviplagalis* (Wlk.)
July 5, 1991 Count 1
- 5571 *Condyolomia partipalis* Grt.
July 4–Aug. 7, 1989 Count 40
- 5577 *Epipaschia superatalis* Clem.
June 20, 1991–July 22, 1988 Count 4
- 5606 *Tetralopha asperatella* (Clem.)
July 20, 1990 Count 1
- 5622 *Galleria mellonella* (L.)
July 12–Sep. 13, 1991 Count 4
- 5997 *Euzophera ostricolorella* Hulst
June 15, 1988–Aug. 16, 1990 Count 15
- 6053 *Peoria approximella* (Wlk.)
July 3, 1992–Aug. 16, 1990 Count 14

Family THYRIDIDAE

- 6079 *Dysodia granulata* (Neum.)
Aug. 21, 1989 Count 1

Family PTEROPHORIDAE

- 6226 *Oidaematophorus unicolor* (B. & McD.)
June 4, 1989 Count 3

Family THYATIRIDAE

- 6235 *Habrosyne scripta* (Gosse)
June 15, 1988 Count 1
- 6237 *Pseudothyatira cymatophoroides* (Gn.)
June 26, 1992 Count 1

Family DREPANIDAE

- 6251 *Drepana arcuata* Wlk.
June 1–Aug. 9, 1990 Count 11
- 6253 *Eudeilinia herminiata* (Gn.)
Aug. 7, 1992–Aug. 14, 1989 Count 2
- 6255 *Oreta rosea* (Wlk.)
June 6, 1991–Aug. 21, 1989 Count 22

Family GEOMETRIDAE

- 6261 *Helionata cycladata* G. & R.
May 30, 1991–June 15, 1988 Count 3
- 6270 *Protitame virginalis* (Hulst)
June 15, 1988–Aug. 7, 1989 Count 5
- 6273 *Itame pustularia* (Gn.)
June 13, 1991–Sep. 9, 1989 Count 3733
- 6278 *Itame evagaria* (Hulst)
July 13, 1990 Count 1
- 6299 *Itame coartaria* (Hulst)
June 20, 1991–July 10, 1992 Count 6
- 6303 *Itame subcessaria* (Wlk.)
July 15, 1988–July 24, 1992 Count 3
- 6335+ *Semiothisa aequiferaria* (Wlk.)
May 30, 1991–Aug. 9, 1990 Count 40
- 6340 *Semiothisa minorata* (Pack.)
July 19, 1991–July 20, 1990 Count 2
- 6342 *Semiothisa bisignata* (Wlk.)
June 22, 1988–Aug. 16, 1991 Count 13
- 6344+ *Semiothisa signaria* (Hbn.)
June 15–Aug. 9, 1990 Count 11
- 6386 *Semiothisa ocellinata* (Gn.)
July 10, 1989–Aug. 26, 1988 Count 2
- 6405 *Semiothisa gnophosaria* (Gn.)
June 15, 1988–Aug. 2, 1991 Count 7
- 6583 *Anacamptodes ephyraria* (Wlk.)
June 27, 1991–July 24, 1989 Count 77
- 6584 *Anacamptodes humaria* (Gn.)
July 15, 1988–July 31, 1989 Count 6
- 6586 *Anacamptodes defectaria* (Gn.)
July 13, 1990–Aug. 19, 1988 Count 2
- 6588 *Iridopsis larvaria* (Gn.)
May 30, 1991–Aug. 16, 1990 Count 8
- 6590 *Anavitrinella pampinaria* (Gn.)
May 30, 1991–Sep. 24, 1988 Count 55
- 6597 *Ectropis crepuscularia* (D. & S.)
June 5, 1992–July 26, 1991 Count 41
- 6598 *Protoarmia porcelaria* (Gn.)
June 6, 1991–Sep. 10, 1992 Count 19
- 6599 *Epinecis hortaria* (F.)
May 21, 1989–Aug. 9, 1990 Count 31
- 6620+ *Melanolophia canadaria* (Gn.)
May 21–Aug. 14, 1989 Count 120

- 6640a *Biston betularia cognataria* (Gn.)
June 29, 1988 Count 1
- 6654 *Hypagyrtis unipunctata* (Haw.)
May 30, 1991–Aug. 24, 1990 Count 27
- 6655 *Hypagyrtis esther* (Barnes)
May 30, 1991–Sep. 7, 1990 Count 176
- 6667 *Lomographa vestaliata* (Gn.)
May 28–July 10, 1992 Count 56
- 6668 *Lomographa glomeraria* (Grt.)
May 21, 1989 Count 1
- 6677 *Cabera erythemaria* Gn.
May 21, 1989–Aug. 27, 1992 Count 27
- 6678 *Cabera variolaria* Gn.
June 1, 1988–June 8, 1990 Count 2
- 6720 *Lytoisitis unitaria* (H.-S.)
June 20, 1991–July 10, 1989 Count 82
- 6724 *Euchlaena serrata* (Drury)
July 3, 1992–July 31, 1989 Count 7
- 6725 *Euchlaena nuzaria* (Wlk.)
May 30, 1991–July 8, 1988 Count 38
- 6729 *Euchlaena johnsonaria* (Fitch)
June 5, 1992–Aug. 21, 1989 Count 6
- 6739 *Euchlaena irraria* (B. & McD.)
June 15, 1988 Count 2
- 6740+ *Xanthotype urticaria* Swett
May 30, 1991–Aug. 21, 1989 Count 33
- 6753+ *Pero honestaria* (Wlk.)
May 18, 1988–Aug. 27, 1992 Count 81
- 6763 *Nacophora quernaria* (J.E. Smith)
June 1–June 22, 1988 Count 4
- 6796 *Campaea perlata* (Gn.)
May 30, 1991–Sep. 14, 1990 Count 184
- 6797 *Emmos magnaria* Gn.
Sep. 13, 1991–Sep. 14, 1990 Count 2
- 6798 *Emmos subsignaria* (Hbn.)
June 20, 1991–Aug. 7, 1992 Count 107
- 6812 *Homochlodes fritillaria* (Gn.)
July 13, 1990 Count 1
- 6819 *Metanema inatomaria* Gn.
June 22, 1988–Aug. 27, 1992 Count 2
- 6822 *Metarranthis dnaria* (Gn.)
May 21–June 4, 1989 Count 3
- 6823 *Metarranthis angularia* B. & McD.
June 8, 1990–June 20, 1991 Count 4
- 6825 *Metarranthis indeclinata* (Wlk.)
June 5–June 19, 1992 Count 6
- 6826 *Metarranthis hypocharia* (H.-S.)
May 30, 1991–July 10, 1992 Count 118
- 6827 *Metarranthis refractaria* (Gn.)
July 3, 1992 Count 2
- 6828 *Metarranthis homuraria* (G. & R.)
June 1, 1988 Count 1
- 6834 *Cepphis decoloraria* (Hulst)
June 4–July 17, 1989 Count 8
- 6835 *Cepphis armataria* (H.-S.)
May 30–July 5, 1991 Count 3

- 6836 *Anagoga occiduaria* (Wlk.)
July 20, 1990–Aug. 14, 1989 Count 11
- 6838+ *Probole amicaria* (H.-S.)
May 28, 1992–Aug. 16, 1990 Count 106
- 6840 *Plagodis serinaria* H.-S.
May 18, 1988–June 29, 1990 Count 127
- 6841 *Plagodis kuetzingi* (Grt.)
Aug. 2, 1991 Count 1
- 6842 *Plagodis phlogosaria* (Gn.)
July 15, 1988–July 27, 1990 Count 2
- 6843 *Plagodis fervidaria* (H.-S.)
July 5, 1991–Aug. 7, 1992 Count 10
- 6844 *Plagodis alcoalaria* (Gn.)
May 18, 1988–Aug. 9, 1990 Count 54
- 6884 *Besna endropiaria* (G. & R.)
May 30, 1991–July 8, 1988 Count 35
- 6885 *Besna quercivoraria* (Gn.)
May 21–Sep. 2, 1989 Count 82
- 6888 *Lambdina fiscellaria* (Gn.)
Aug. 16, 1991–Sep. 25, 1992 Count 7
- 6894a *Lambdina fervidaria athasaria* (Wlk.)
Aug. 7, 1992 Count 1
- 6912 *Sicya macularia* (Harr.)
June 13, 1991–July 10, 1992 Count 22
- 6941 *Eusarca confusaria* Hbn.
June 27, 1991–July 20, 1990 Count 19
- 6963 *Tetracis crocallata* Gn.
July 8, 1988 Count 1
- 6964 *Tetracis cachexiata* Gn.
May 30, 1991–June 26, 1992 Count 63
- 6965 *Eugonobapta nivosaria* (Gn.)
June 13, 1991–July 31, 1992 Count 127
- 6966 *Eutrapela clemataria* (J.E. Smith)
May 18, 1988–Aug. 7, 1992 Count 93
- 6982 *Prochoerodes transversata* (Drury)
June 20, 1991–Sep. 25, 1992 Count 106
- 6987 *Antepione thisoaria* (Gn.)
July 19, 1991 Count 1
- 7009 *Nematocampa limbata* (Haw.)
June 13, 1991–Sep. 9, 1989 Count 131
- 7046+ *Nemoria bistriaria* Hbn.
May 28–Aug. 14, 1989 Count 54
- 7047 *Nemoria rubrifrontaria* (Pack.)
June 15, 1988 Count 1
- 7048 *Nemoria niuosaria* (Gn.)
June 4, 1989–Aug. 30, 1991 Count 3
- 7053 *Dichorda iridaria* (Gn.)
May 28–July 31, 1989 Count 3
- 7058 *Synchlora aerata* (F.)
May 30–Aug. 30, 1991 Count 10
- 7071 *Chlorochlamys chloroleucaria* (Gn.)
June 26, 1989–Sep. 7, 1990 Count 5
- 7084 *Hethemia pistasciaria* (Gn.)
June 1, 1988 Count 1
- 7132 *Pleuroprucha insulsaria* (Gn.)
May 30–Aug. 30, 1991 Count 17
- 7136 *Cyclophora packardii* (Prout)
May 30–Sep. 13, 1991 Count 11
- 7139 *Cyclophora pendulinaria* (Gn.)
May 30, 1991–Sep. 9, 1989 Count 77
- 7146 *Haematopis grataria* (F.)
Aug. 7, 1992–Sep. 9, 1989 Count 2
- 7157 *Scopula cacuminiaria* (Morr.)
May 30, 1991–Aug. 21, 1992 Count 33
- 7159 *Scopula limboundata* (Haw.)
May 30, 1991–Aug. 21, 1989 Count 147
- 7165 *Scopula quadrilineata* (Pack.)
May 30, 1991 Count 2
- 7169 *Scopula inductata* (Gn.)
June 5, 1992–Aug. 30, 1991 Count 13
- 7189 *Dysstroma hersiliata* (Gn.)
June 20, 1991–July 3, 1992 Count 2
- 7196+ *Eulithis diversilineata* (Hbn.)
June 29, 1990–Sep. 4, 1992 Count 12
- 7236+ *Hydriomena renunciata* (Wlk.)
May 18, 1988 Count 6
- 7290 *Coryphista meadii* (Pack.)
July 24, 1989–Sep. 4, 1992 Count 2
- 7292 *Hydria prunivora* (Fgn.)
July 15, 1988 Count 1
- 7368 *Xanthorhoe labradorensis* (Pack.)
Aug. 24, 1990–Sep. 13, 1991 Count 7
- 7388 *Xanthorhoe ferrugata* (Cl.)
June 12, 1989–July 26, 1991 Count 3
- 7390 *Xanthorhoe lacustrata* (Gn.)
July 12, 1991–Sep. 9, 1989 Count 10
- 7394 *Epirrhoe alternata* (Muller)
June 20, 1991–Sep. 9, 1989 Count 5
- 7399a *Euphyia unangulata intermediata* (Gn.)
June 12–Sep. 4, 1992 Count 8
- 7414 *Orthonama obstipata* (F.)
May 21–Sep. 9, 1989 Count 47
- 7416 *Orthonama centrostrigaria* (Woll.)
May 30–Sep. 6, 1991 Count 108
- 7422 *Hydrelia inornata* (Hulst)
May 30, 1991–June 15, 1988 Count 3
- 7423 *Hydrelia albifera* (Wlk.)
May 30, 1991–Aug. 21, 1989 Count 5
- 7430 *Trichodezia albovittata* (Gn.)
May 30, 1991–Aug. 16, 1990 Count 3
- 7440 *Eubaphe mendica* (Wlk.)
June 26–July 24, 1992 Count 8
- 7445 *Horisme intestinata* (Gn.)
July 26, 1991–Aug. 24, 1990 Count 7
- 7474+ *Eupithecia miserulata* Grt.
May 21, 1989–Sep. 24, 1988 Count 140
- 7640 *Lobophora nivergerata* Wlk.
June 1, 1990–July 8, 1988 Count 8
- 7647 *Heterophleps triguttaria* H.-S.
June 26, 1989–July 13, 1990 Count 2
- Family EPIPLEMIDAE**
- 7653 *Calledapteryx dryopterata* Grt.
June 22–Aug. 9, 1990 Count 2

Family MIMALLONIDAE

- 7659 *Lacosoma chiridota* Grt.
June 15, 1988 Count 1

Family APATELODIDAE

- 7663 *Apateles torrefacta* (J.E. Smith)
June 6, 1991–June 29, 1990 Count 4
- 7665 *Olceclostera angelica* (Grt.)
June 20, 1991–July 17, 1992 Count 2

Family LASIOCAMPIDAE

- 7670 *Tolyte velleda* (Stoll)
Aug. 2, 1991–Sep. 24, 1988 Count 10
- 7687 *Phyllodesma americana* (Harr.)
May 21, 1989–July 15, 1988 Count 6
- 7698 *Malacosoma dissiria* Hbn.
June 20, 1991–July 24, 1989 Count 163
- 7701 *Malacosoma americanum* (F.)
June 13, 1991–July 17, 1992 Count 231

Family SATURNIIDAE

- 7715 *Dryocampa rubicunda* (F.)
May 30, 1991–Aug. 5, 1988 Count 52
- 7723 *Anisota virginienensis* (Drury)
June 1, 1988 Count 1
- 7746 *Automeris io* (F.)
May 30, 1991–June 29, 1990 Count 11
- 7757 *Antheraea polyphemus* (Cram.)
June 15, 1988–July 10, 1989 Count 7
- 7758 *Actias luna* (L.)
June 12–June 26, 1989 Count 3
- 7764 *Callosamia promethea* (Drury)
July 31, 1992 Count 1
- 7767 *Hyalophora cecropia* (L.)
June 29, 1990 Count 1

Family SPHINGIDAE

- 7784 *Dolba hyloeus* (Drury)
July 8, 1988 Count 1
- 7787 *Ceratomia undulosa* (Wlk.)
July 5, 1991 Count 1
- 7810 *Sphinx gordius* Cram.
May 30, 1991–June 8, 1990 Count 3
- 7821 *Smerinthus jamaicensis* (Drury)
May 30–July 12, 1991 Count 4
- 7824 *Paonias excrucatus* (J.E. Smith)
May 30, 1991–Aug. 7, 1992 Count 69
- 7825 *Paonias myops* (J.E. Smith)
May 30, 1991–Aug. 14, 1989 Count 14
- 7827 *Loathoe juglandis* (J.E. Smith)
June 27, 1991–July 13, 1990 Count 5
- 7828 *Pachysphinx modesta* (Harr.)
June 15, 1988 Count 1
- 7870 *Sphecodina abbottii* (Swainson)
June 1, 1988 Count 1

Family NOTODONTIDAE

- 7895 *Clostera albogigna* Fitch
June 13–Aug. 30, 1991 Count 12

- 7898 *Clostera strigosa* (Grt.)
July 5–Aug. 16, 1991 Count 6
- 7901 *Clostera apicalis* (Wlk.)
June 1, 1990–Aug. 27, 1992 Count 6
- 7902 *Datana ministra* (Drury)
June 15–July 15, 1988 Count 8
- 7903 *Datana angusii* G. & R.
May 30, 1991–July 17, 1989 Count 11
- 7904+ *Datana drexlii* Hy. Edw.
June 15, 1990–July 17, 1989 Count 8
- 7906+ *Datana contracta* Wlk.
May 30, 1991–Aug. 7, 1992 Count 17
- 7915 *Nadata gibbosa* (J.E. Smith)
May 28, 1989–Aug. 24, 1990 Count 218
- 7919 *Peridea basitriens* (Wlk.)
May 30, 1991–Aug. 24, 1990 Count 19
- 7920 *Peridea angulosa* (J.E. Smith)
May 30, 1991–Sep. 9, 1989 Count 235
- 7922 *Pheosia rimosa* Pack.
July 13, 1990–July 22, 1988 Count 3
- 7926 *Notodonta scitipeunisi* Wlk.
Aug. 14, 1989 Count 1
- 7929 *Nerice bidentata* Wlk.
May 30, 1991–Aug. 14, 1989 Count 6
- 7930 *Ellida caniplaga* (Wlk.)
July 10, 1989 Count 1
- 7931 *Gluphisia septentrionis* Wlk.
June 15, 1988–July 31, 1989 Count 5
- 7936 *Furcula borealis* (Guer.-Meneville)
May 28, 1989–July 19, 1991 Count 5
- 7951+ *Synmerista albifrons* (J.E. Smith)
May 28, 1989–Aug. 27, 1992 Count 98
- 7957 *Dasylophia anguina* (J.E. Smith)
June 8–June 29, 1990 Count 2
- 7958 *Dasylophia thyatiroides* (Wlk.)
May 28, 1989–Aug. 23, 1991 Count 16
- 7975 *Macrurocampa warthesia* (Cram.)
June 20, 1991–Aug. 7, 1992 Count 70
- 7994 *Heterocampa guttivitta* (Wlk.)
May 30, 1991–Aug. 5, 1988 Count 175
- 7995 *Heterocampa biundata* Wlk.
Aug. 9, 1990–Aug. 27, 1992 Count 5
- 7998 *Lochmaeus manteo* Doubleday
June 26, 1992–Aug. 14, 1989 Count 19
- 7999 *Lochmaeus bilineata* (Pack.)
June 8–Aug. 24, 1990 Count 23
- 8005 *Schizura ipomoeae* Doubleday
May 30, 1991–July 17, 1992 Count 7
- 8006 *Schizura badia* (Pack.)
June 12, 1989–Aug. 5, 1988 Count 5
- 8007 *Schizura unicornis* (J.E. Smith)
May 30, 1991–Sep. 7, 1990 Count 63
- 8011 *Schizura leptinoides* (Grt.)
June 12, 1989–Aug. 27, 1992 Count 9
- 8012 *Oligocentria semirufescens* (Wlk.)
June 15, 1990–July 15, 1988 Count 4
- 8017 *Oligocentria lignicolor* (Wlk.)
May 28, 1992–Aug. 16, 1990 Count 10

Family ARCTIIDAE

- 8045.1 *Crambidia pallida* Pack.
July 8, 1988–Sep. 4, 1992..... Count 70
- 8090 *Hypoprepia fucosa* Hbn.
July 5, 1991–Aug. 16, 1990..... Count 71
- 8104 *Comachara cadburyi* Franc.
June 5, 1992..... Count 1
- 8107 *Haploa chymene* (Brown)
July 5, 1991–July 31, 1992..... Count 8
- 8121+ *Holomelina aurantiaca* (Hbn.)
May 30–Aug. 30, 1991..... Count 139
- 8129 *Pyrrharctia isabella* (J.E. Smith)
May 30, 1991–Sep. 10, 1992..... Count 60
- 8133 *Spilosoma latipennis* Stretch
May 30, 1991–June 29, 1990..... Count 14
- 8134 *Spilosoma congrua* Wlk.
May 21, 1989–Sep. 13, 1991..... Count 249
- 8137 *Spilosoma virginica* (F.)
May 30, 1991–Aug. 24, 1990..... Count 76
- 8140 *Hyphantria cunea* (Drury)
June 26, 1992–July 8, 1988..... Count 5
- 8156 *Phragmatobia fuliginosa* (L.)
July 5, 1991–Aug. 27, 1992..... Count 28
- 8169+ *Apantesis phalerata* (Harr.)
May 30–Sep. 13, 1991..... Count 70
- 8197 *Apantesis virgo* (L.)
July 12, 1991–July 27, 1990..... Count 8
- 8203+ *Halysidota tessellaris* (J.E. Smith)
June 6 1991–Aug. 7, 1992..... Count 458
- 8211 *Lophocampa caryae* Harr.
May 30, 1991–June 26, 1992..... Count 47
- 8230 *Cynia tenera* Hbn.
June 5, 1992–Aug. 2, 1991..... Count 16
- 8231 *Cynia oregonensis* (Stretch)
June 15–Aug. 5, 1988..... Count 3
- 8238 *Euchaetes egle* (Drury)
June 6, 1991–Aug. 5, 1988..... Count 14
- 8262 *Ctenucha virginica* (Esp.)
May 30, 1991–June 15, 1990..... Count 5
- 8267 *Ciseps fulvicollis* (Hbn.)
May 30, 1991–Sep. 21, 1990..... Count 221

Family LYMANTRIIDAE

- 8294 *Dasychira vagans* (B. & McD.)
July 27, 1990..... Count 1
- 8296 *Dasychira basiflava* (Pack.)
July 12, 1991–Aug. 16, 1990..... Count 28
- 8302 *Dasychira obliquata* (G. & R.)
July 26, 1991–Aug. 14, 1989..... Count 15
- 8314 *Orygia definita* Pack.
July 5, 1991–Aug. 31, 1990..... Count 7
- 8316 *Orygia leucostigma* (J.E. Smith)
June 20, 1991–Sep. 21, 1990..... Count 11
- 8318 *Lymantria dispar* (L.)
July 5, 1991–Aug. 27, 1992..... Count 182

Family NOCTUIDAE

- 8322 *Idia americalis* (Gn.)
May 30, 1991–Sep. 21, 1990..... Count 63

- 8323+ *Idia aemula* Hbn.
May 30, 1991–Sep. 21, 1990..... Count 115
- 8326 *Idia roundalis* (Wlk.)
June 20, 1991–Sep. 10, 1992..... Count 530
- 8327 *Idia forbesi* (French)
June 12, 1989–Aug. 3, 1990..... Count 53
- 8329 *Idia diminutis* (B. & McD.)
June 20–Aug. 30, 1991..... Count 244
- 8330 *Idia scobialis* (Grt.)
July 13–July 20, 1990..... Count 14
- 8333 *Idia denticulalis* (Harv.)
July 12, 1991..... Count 2
- 8334 *Idia lubricalis* (Gey.)
June 22, 1990–Sep. 9, 1989..... Count 24
- 8338 *Phalaenophana pyramusalis* (Wlk.)
June 5, 1992–Aug. 14, 1989..... Count 6
- 8340 *Zanclognatha lituralis* (Hbn.)
June 1–Sep. 7, 1990..... Count 22
- 8345 *Zanclognatha laevigata* (Grt.)
June 20, 1991–Sep. 4, 1992..... Count 33
- 8348 *Zanclognatha pedipalpis* (Gn.)
June 15, 1990–June 22, 1988..... Count 2
- 8349 *Zanclognatha protumnusalis* (Wlk.)
July 22, 1988–Sep. 13, 1991..... Count 5
- 8351 *Zanclognatha cruralis* (Gn.)
June 26–July 17, 1989..... Count 14
- 8352+ *Zanclognatha jacchusalis* (Wlk.)
June 12, 1989–Sep. 21, 1990..... Count 207
- 8355 *Chytolita morbidalis* (Gn.)
May 30, 1991–July 10, 1992..... Count 39
- 8356 *Chytolita petrealis* Grt.
June 5–July 24, 1992..... Count 11
- 8357 *Macrochilo absorptalis* (Wlk.)
June 22, 1990–Aug. 7, 1992..... Count 42
- 8357.1 *Macrochilo hypocritalis* Fgn.
June 20–Sep. 13, 1991..... Count 5
- 8358 *Macrochilo litophora* (Grt.)
June 20, 1991–July 20, 1990..... Count 15
- 8360 *Macrochilo orciferalis* (Wlk.)
June 15, 1988–Aug. 27, 1992..... Count 10
- 8361 *Macrochilo louisiana* (Fbs.)
May 30, 1991..... Count 3
- 8362 *Phalaenostola metonalis* (Wlk.)
May 30, 1991–Aug. 27, 1992..... Count 19
- 8363 *Phalaenostola eumehusalis* (Wlk.)
June 27, 1991–Aug. 9, 1990..... Count 5
- 8364 *Phalaenostola larentioides* Grt.
June 26, 1992–Sep. 13, 1991..... Count 13
- 8365 *Phalaenostola hanhami* (Sm.)
July 13, 1990..... Count 1
- 8370 *Bleptina caradrinalis* Gn.
June 20, 1991–July 31, 1989..... Count 14
- 8378 *Renia salusalis* (Wlk.)
July 17, 1992–July 19, 1991..... Count 5
- 8379 *Renia factiosalis* (Wlk.)
June 15, 1988–Aug. 21, 1992..... Count 57
- 8381 *Renia discoloralis* Gn.
June 29, 1990–Sep. 4, 1992..... Count 65

8386	<i>Renia adspersgillus</i> (Bosc.) June 26–Sep. 9, 1989	Count 44	8588	<i>Panopoda carneicosta</i> Gn. June 22–July 15, 1988	Count 4
8387	<i>Renia sobrialis</i> (Wlk.) June 20, 1991–July 24, 1989	Count 8	8689	<i>Zale lunata</i> (Drury) July 13–July 20, 1990	Count 4
8393	<i>Lascoria ambignalis</i> Wlk. June 4, 1989–Aug. 16, 1991	Count 6	8697	<i>Zale minerea</i> (Gn.) May 21, 1989–July 15, 1988	Count 14
8397	<i>Palthis angulalis</i> (Hbn.) May 30, 1991–Sep. 7, 1990	Count 15	8700	<i>Zale squamularis</i> (Drury) May 18, 1988	Count 1
8398	<i>Palthis asopialis</i> (Gn.) May 30–Sep. 13, 1991	Count 40	8704+	<i>Zale helata</i> (Sm.) June 22, 1990	Count 1
8404	<i>Rivula propinquialis</i> Gn. May 30–Sep. 13, 1991	Count 62	8716	<i>Zale unilineata</i> (Grt.) June 15, 1988	Count 1
8411	<i>Colobochyla interpuncta</i> (Grt.) June 12, 1989–July 12, 1991	Count 7	8717	<i>Zale horrida</i> Hbn. May 30, 1991–July 4, 1989	Count 6
8412	<i>Melanomima auricinctaria</i> Grt. May 30, 1991–Aug. 16, 1990	Count 25	8721	<i>Allotria elonympha</i> (Hbn.) May 30–Aug. 16, 1991	Count 24
8421	<i>Hypenodes fractilinea</i> (Sm.) May 30, 1991–Sep. 10, 1992	Count 96	8727	<i>Parallelia bistriaris</i> Hbn. May 30, 1991–Sep. 4, 1992	Count 19
8426	<i>Dyspyralis illocata</i> Warr. July 5–July 19, 1991	Count 5	8738+	<i>Caenurgina crassiuscula</i> (Haw.) June 27–Sep. 13, 1991	Count 27
8427	<i>Dyspyralis puncticosta</i> (Sm.) July 5, 1991–July 31, 1989	Count 23	8764	<i>Argyrostromis anilis</i> (Drury) July 4, 1989	Count 1
8428	<i>Dyspyralis nigella</i> (Stkr.) July 5, 1991–Aug. 5, 1988	Count 73	8778	<i>Catocala habilis</i> Grt. Sep. 21, 1990–Sep. 25, 1992	Count 3
8430	<i>Parahypenodes quadralis</i> B. & McD. June 20, 1991	Count 1	8779	<i>Catocala serena</i> Edw. Aug. 27, 1992	Count 1
8441	<i>Bomolocha manalis</i> (Wlk.) June 8, 1990–Sep. 10, 1988	Count 32	8784	<i>Catocala obscura</i> Stkr. Aug. 27, 1992–Sep. 21, 1990	Count 2
8442	<i>Bomolocha baltimoralis</i> (Gn.) May 28, 1992–Sep. 9, 1989	Count 69	8785	<i>Catocala residua</i> Grt. Aug. 9–Sep. 7, 1990	Count 3
8443	<i>Bomolocha bijugalis</i> (Wlk.) Sep. 13, 1991	Count 1	8788	<i>Catocala resecta</i> Grt. Aug. 16, 1990–Sep. 24, 1988	Count 7
8444	<i>Bomolocha palparia</i> (Wlk.) June 15, 1988–Aug. 14, 1989	Count 3	8790	<i>Catocala dejecta</i> Stkr. Sep. 14, 1990	Count 1
8445	<i>Bomolocha abalienalis</i> (Wlk.) June 5, 1992	Count 1	8795	<i>Catocala palaeogama</i> Gn. Aug. 2, 1991	Count 1
8447	<i>Bomolocha madefactalis</i> (Gn.) July 5, 1991–July 13, 1990	Count 2	8801	<i>Catocala ilia</i> (Cram.) July 12, 1991–Aug. 26, 1988	Count 7
8448	<i>Bomolocha sordidula</i> (Grt.) July 12, 1991	Count 1	8802	<i>Catocala cerogama</i> Gn. Sep. 2, 1989	Count 1
8465	<i>Plathypena scabra</i> (F.) June 15, 1990–Sep. 25, 1992	Count 15	8832	<i>Catocala cara</i> Gn. Sep. 9, 1989	Count 1
8479	<i>Spargaloma sexpunctata</i> Grt. June 15–Aug. 19, 1988	Count 12	8846	<i>Catocala sordida</i> Grt. July 12, 1991–Aug. 21, 1989	Count 9
8490	<i>Pangrapta decoralis</i> Hbn. May 30, 1991–Sep. 9, 1989	Count 75	8847	<i>Catocala gracilis</i> Edw. July 13, 1990	Count 1
8491	<i>Ledaea perditalis</i> (Wlk.) May 30, 1991–Sep. 7, 1990	Count 184	8857	<i>Catocala ultionia</i> (Hbn.) July 20, 1990–Aug. 27, 1992	Count 15
8499	<i>Metalectra discalis</i> (Grt.) July 15, 1988–Aug. 9, 1990	Count 2	8858	<i>Catocala crataegi</i> Saund. July 22, 1988–Aug. 7, 1992	Count 2
8514	<i>Scolecocampa libinra</i> (Gey.) June 20, 1991–Aug. 7, 1992	Count 37	8863	<i>Catocala mira</i> Grt. July 13, 1990–Aug. 27, 1992	Count 27
8536	<i>Calyptra canadensis</i> (Bethune) July 10, 1992	Count 1	8864	<i>Catocala grynea</i> (Cram.) July 5, 1991–Sep. 9, 1989	Count 38
8555	<i>Scoliopteryx libatrix</i> (L.) May 14, 1989–June 22, 1988	Count 2	8865	<i>Catocala praeclara</i> G. & R. July 12, 1991–Aug. 14, 1989	Count 10
8587	<i>Panopoda rufimargo</i> (Hbn.) June 20, 1991–Aug. 7, 1992	Count 58	8867	<i>Catocala blandula</i> Hulst July 12, 1991–July 24, 1989	Count 2

- 8878 *Catocala amica* (Hbn.)
July 12, 1991–Sep. 9, 1989. Count 7
- 8878.1 *Catocala lineella* Grt.
July 12, 1991–Aug. 27, 1992. Count 3
- 8898 *Allagrapha aerea* (Hbn.)
June 8–Sep. 21, 1990. Count 26
- 8904 *Chrysanypha formosa* (Grt.)
June 26, 1992–June 29, 1990. Count 2
- 8908 *Autographa precationis* (Gn.)
May 28, 1989–Sep. 25, 1992. Count 16
- 8924 *Anagrapha falcifera* (Kby.)
July 17, 1989–July 26, 1991. Count 3
- 8955 *Marathyssa inficita* (Wlk.)
June 15, 1988. Count 1
- 8956 *Marathyssa basalis* Wlk.
May 21–May 28, 1989. Count 2
- 8957 *Paectes oculatrix* (Gn.)
June 19–Sep. 9, 1989. Count 7
- 8970 *Baileya ophthalmica* (Gn.)
May 21, 1989–June 26, 1992. Count 44
- 8971 *Baileya dormitans* (Gn.)
May 30–Aug. 2, 1991. Count 17
- 8972 *Baileya levitans* (Sm.)
June 12–July 24, 1989. Count 11
- 8975 *Nycteola frigidana* (Wlk.)
June 4, 1989–Aug. 3, 1990. Count 3
- 8983 *Meganola minuscula* (Zell.)
May 21, 1989–Aug. 16, 1990. Count 124
- 8983.1 *Meganola phylla* (Dyar)
May 28–July 31, 1989. Count 7
- 8983.2 *Meganola spodia* Franc.
July 3, 1992–July 4, 1989. Count 3
- 8990 *Nola cilicoides* (Grt.)
June 15, 1988. Count 1
- 8992 *Nola triquetrana* (Fitch)
May 21, 1989. Count 2
- 9037 *Hyperstrotia pervertens* (B. & McD.)
May 30, 1991–Aug. 3, 1990. Count 34
- 9038 *Hyperstrotia villificans* (B. & McD.)
June 22, 1990–July 12, 1991. Count 25
- 9040 *Hyperstrotia secta* (Grt.)
June 22, 1990–Aug. 2, 1991. Count 9
- 9046 *Lithacodia bellicula* Hbn.
June 20, 1991–Aug. 24, 1990. Count 3
- 9047 *Lithacodia muscosula* (Gn.)
May 30, 1991–Sep. 9, 1989. Count 269
- 9048 *Lithacodia albidula* (Gn.)
June 22, 1988–Aug. 21, 1989. Count 36
- 9051 *Lithacodia musta* (G. & R.)
July 29, 1988. Count 1
- 9053 *Pseudeustrotia cameola* (Gn.)
May 30, 1991–Sep. 25, 1992. Count 125
- 9055.1 *Maliattha synochitis* (G. & R.)
May 30, 1991–July 22, 1988. Count 29
- 9055.3 *Anterastria teratophora* (H.-S.)
June 15, 1988–June 22, 1990. Count 2
- 9056 *Homophoberia cristata* Morr.
May 30, 1991–Aug. 7, 1992. Count 20
- 9057 *Homophoberia apicosa* (Haw.)
May 30, 1991–Sep. 9, 1989. Count 62
- 9062 *Cerma cerintha* (Tr.)
May 30, 1991–Aug. 5, 1988. Count 14
- 9065 *Leuconycta diptheroides* (Gn.)
June 15, 1990–Aug. 7, 1992. Count 14
- 9066 *Leuconycta lepidula* (Grt.)
May 30, 1991–Aug. 5, 1988. Count 22
- 9090 *Tarachidia candefacta* (Hbn.)
June 15, 1988–Aug. 21, 1989. Count 14
- 9095 *Tarachidia erastrioides* (Gn.)
June 1, 1988–Aug. 27, 1992. Count 15
- 9185 *Colocasía propinquilinea* (Grt.)
May 30, 1991–June 26, 1992. Count 42
- 9189 *Charadra deridens* (Gn.)
May 18, 1988. Count 1
- 9193 *Raphia frater* Grt.
June 1, 1988–Aug. 7, 1992. Count 18
- 9200 *Acronicta americana* (Harr.)
May 30, 1991–July 20, 1990. Count 18
- 9219 *Acronicta connecta* Grt.
June 22, 1988–June 27, 1991. Count 2
- 9227 *Acronicta laetifica* Sm.
June 15, 1988–Aug. 21, 1992. Count 3
- 9229 *Acronicta hasta* Gn.
May 30, 1991–July 31, 1992. Count 16
- 9235 *Acronicta spinigera* Gn.
June 12, 1989–June 29, 1990. Count 8
- 9236 *Acronicta morula* G. & R.
June 15, 1990. Count 1
- 9237 *Acronicta interrupta* Gn.
July 17–Aug. 21, 1989. Count 3
- 9238 *Acronicta lobeliae* Gn.
May 18, 1988–Aug. 7, 1989. Count 3
- 9242 *Acronicta exilis* Grt.
June 22, 1988–Aug. 14, 1989. Count 4
- 9243 *Acronicta ovata* Grt.
June 6, 1991–Aug. 7, 1989. Count 81
- 9244 *Acronicta modica* Wlk.
May 30, 1991–Aug. 5, 1988. Count 48
- 9245+ *Acronicta haesitata* (Grt.)
May 30–Aug. 16, 1991. Count 212
- 9246 *Acronicta clarescens* Gn.
July 31–Aug. 7, 1989. Count 2
- 9251 *Acronicta retardata* (Wlk.)
June 8–July 13, 1990. Count 5
- 9259 *Acronicta noctivaga* Grt.
June 26, 1992. Count 1
- 9261 *Acronicta impressa* Wlk.
July 29–Aug. 26, 1988. Count 5
- 9272 *Acronicta obliuina* (J.E. Smith)
July 27, 1990–July 31, 1989. Count 2
- 9285 *Polygrammate hebraeicum* Hbn.
May 30–Aug. 2, 1991. Count 119
- 9299 *Eudryas unio* (Hbn.)
June 22, 1990–Aug. 14, 1989. Count 4
- 9301 *Eudryas grata* (F.)
July 8, 1988–July 24, 1989. Count 6

9328	<i>Apamea nigrrior</i> (Sm.) June 13, 1991–July 3, 1992.....	Count 4
9329	<i>Apamea cariosa</i> (Gn.) July 15, 1988–July 17, 1992.....	Count 2
9332	<i>Apamea vulgaris</i> (G. & R.) June 15, 1990–June 27, 1991.....	Count 3
9341	<i>Apamea vulnosa</i> (Grt.) June 26, 1992.....	Count 1
9364	<i>Apamea sordens</i> (Hufn.) June 12, 1989–June 26, 1992.....	Count 4
9427	<i>Meropleon diversicolor</i> (Morr.) Aug. 21, 1989–Sep. 21, 1990.....	Count 31
9428	<i>Meropleon ambifuscum</i> (Newman) Sep. 9, 1989.....	Count 1
9451	<i>Archana laeta</i> (Morr.) July 20, 1990.....	Count 1
9454	<i>Amphipoea velata</i> (Wlk.) July 10, 1989–July 27, 1990.....	Count 4
9457+	<i>Amphipoea americana</i> (Speyer) July 20, 1990–Aug. 21, 1992.....	Count 4
9471	<i>Papaipema arctivorens</i> Hamp. Sep. 7–Sep. 21, 1990.....	Count 2
9482	<i>Papaipema speciosissima</i> (G. & R.) Sep. 13, 1991–Sep. 24, 1988.....	Count 5
9483	<i>Papaipema iniquaenita</i> (G. & R.) Aug. 26, 1988–Sep. 25, 1992.....	Count 8
9485	<i>Papaipema baptisiae</i> (Bird) Aug. 24, 1990–Sep. 13, 1991.....	Count 3
9486	<i>Papaipema birdi</i> (Dyar) Sep. 9, 1989–Sep. 25, 1992.....	Count 2
9503	<i>Papaipema rigida</i> (Grt.) Sep. 13, 1991.....	Count 1
9505	<i>Papaipema cernsata</i> (Grt.) Sep. 21, 1990–Sep. 25, 1992.....	Count 4
9523	<i>Bellura gortynoides</i> Wlk. July 31, 1989–Aug. 7, 1992.....	Count 5
9525	<i>Bellura obliqua</i> (Wlk.) June 4–June 12, 1989.....	Count 6
9545	<i>Euplexia benesimilis</i> McD. May 30, 1991–Aug. 14, 1989.....	Count 41
9546	<i>Phlogophora iris</i> Gn. June 22, 1988.....	Count 1
9547	<i>Phlogophora periculosa</i> Gn. Aug. 14, 1989–Sep. 13, 1991.....	Count 12
9551	<i>Enargia mephisto</i> Franc. June 20, 1991–June 22, 1990.....	Count 2
9555	<i>Ipimorpha pleonectusa</i> Grt. July 19, 1991–Sep. 9, 1989.....	Count 18
9556	<i>Chytonix palliatricula</i> (Gn.) June 1, 1988–July 31, 1989.....	Count 37
9578	<i>Hyppa xylinoides</i> (Gn.) June 8, 1988–Sep. 6, 1991.....	Count 13
9618	<i>Phosphila turbulenta</i> Hbn. June 27–July 12, 1991.....	Count 6
9619	<i>Phosphila mischoides</i> (Gn.) June 19, 1989–July 12, 1991.....	Count 5
9631	<i>Callopietria mollissima</i> (Gn.) June 12, 1992–Aug. 24, 1990.....	Count 21
9638	<i>Amphipyra pyramidoides</i> Gn. July 12, 1991–Sep. 25, 1992.....	Count 82
9647	<i>Athetis miranda</i> (Grt.) June 5, 1992–Aug. 5, 1988.....	Count 3
9650	<i>Anorthodes tarda</i> (Gn.) May 28–Sep. 25, 1992.....	Count 57
9661	<i>Crambodes talidiformis</i> Gn. June 4–Sep. 9, 1989.....	Count 7
9662	<i>Balsa malana</i> (Fitch) June 15, 1988–Aug. 14, 1989.....	Count 6
9663	<i>Balsa tristrigella</i> (Wlk.) May 30, 1991–July 15, 1988.....	Count 94
9664	<i>Balsa labecula</i> (Grt.) May 30, 1991–July 10, 1989.....	Count 19
9666	<i>Spodoptera frugiperda</i> (J.E. Smith) Sep. 7–Sep. 21, 1990.....	Count 3
9681	<i>Elaphria festivoideis</i> (Gn.) June 12, 1989–July 3, 1992.....	Count 7
9688	<i>Galgula partita</i> Gn. June 1, 1988–Sep. 9, 1989.....	Count 16
9689	<i>Perigea xanthioides</i> Gn. June 26, 1989–July 15, 1988.....	Count 6
9690	<i>Condica videns</i> (Gn.) June 1, 1990–Aug. 21, 1989.....	Count 22
9696	<i>Condica vecors</i> (Gn.) June 8, 1990–July 12, 1991.....	Count 5
9720	<i>Ogdoconta cinereola</i> (Gn.) May 30–Sep. 13, 1991.....	Count 26
9725	<i>Stiriodes obtusa</i> (H.-S.) July 17, 1992.....	Count 1
9815	<i>Cosmia calami</i> (Harv.) June 27, 1991–Aug. 7, 1992.....	Count 114
9818	<i>Amolita fessa</i> Grt. June 20, 1991–July 24, 1992.....	Count 29
9957	<i>Suira bicolorago</i> (Gn.) Sep. 21, 1990–Sep. 25, 1992.....	Count 2
9961	<i>Anathix ralla</i> (G. & R.) May 30, 1991–Sep. 25, 1992.....	Count 37
9962	<i>Anathix puta</i> (G. & R.) Sep. 2, 1989.....	Count 1
10005	<i>Feralia jocosca</i> (Gn.) July 3, 1992.....	Count 1
10019	<i>Psaphida resmians</i> Wlk. May 7, 1989.....	Count 1
10033	<i>Catabena lineolata</i> Wlk. June 27, 1991–Aug. 7, 1992.....	Count 4
10059	<i>Homohadena badistriga</i> (Grt.) July 10, 1989–July 29, 1988.....	Count 3
10194	<i>Cucullia lucifuga</i> (D. & S.) July 8, 1988.....	Count 1
10200	<i>Cucullia asteroides</i> Gn. Aug. 7, 1989.....	Count 1
10276	<i>Polia imbrifera</i> (Gn.) June 29, 1988–July 10, 1989.....	Count 5
10288+	<i>Polia detracta</i> (Wlk.) May 30, 1991–Aug. 24, 1990.....	Count 393
10292	<i>Melanchnra adjuncta</i> (Gn.) June 1, 1988–Aug. 9, 1990.....	Count 2

- 10299 *Lacanobia subjuncta* (G. & R.)
June 8, 1988..... Count 2
- 10300 *Spiranater grandis* (Gn.)
June 26, 1989..... Count 1
- 10397 *Lacinipolia renigera* (Steph.)
June 1, 1988–Sep. 25, 1992..... Count 55
- 10405 *Lacinipolia lorea* (Gn.)
June 6, 1991–July 4, 1989..... Count 35
- 10436 *Aletia oxygala* (Grt.)
May 30, 1991–Aug. 14, 1989..... Count 16
- 10438 *Pseudaletia unipuncta* (Haw.)
May 14, 1989–Sep. 10, 1988..... Count 41
- 10440 *Leucania linita* Gn.
July 19, 1991..... Count 1
- 10444+ *Leucania phragmatidicola* Gn.
June 6–Sep. 13, 1991..... Count 9
- 10446+ *Leucania multilinea* Wlk.
May 30–Aug. 30, 1991..... Count 23
- 10447 *Leucania commoides* Gn.
July 20, 1990–Aug. 2, 1991..... Count 2
- 10461+ *Leucania ursula* (Fbs.)
May 30, 1991–Aug. 27, 1992..... Count 41
- 10501 *Crocigrapha normani* (Grt.)
May 18, 1988–June 8, 1990..... Count 5
- 10521 *Morrisonia confusa* (Hbn.)
May 18, 1988–June 8, 1990..... Count 5
- 10521.1 *Morrisonia latex* (Gn.)
June 6, 1991–July 6, 1990..... Count 12
- 10524 *Nephelodes minians* Gn.
Aug. 21, 1989–Sep. 21, 1990..... Count 130
- 10532 *Homorthodes furfurata* (Grt.)
June 20, 1991–July 31, 1992..... Count 6
- 10578 *Pseudorthodes vecors* (Gn.)
June 1, 1988–Sep. 13, 1991..... Count 40
- 10585 *Orthodes crenulata* (Butler)
Sep. 4, 1992..... Count 1
- 10587 *Orthodes cynica* Gn.
May 30, 1991–July 22, 1988..... Count 97
- 10627 *Tricholia signata* (Wlk.)
Aug. 19–Sep. 10, 1988..... Count 15
- 10663 *Agrotis ipsilon* (Hufn.)
June 8–Sep. 10, 1988..... Count 24
- 10674+ *Feltia subgothica* (Haw.)
July 29, 1988–Sep. 4, 1992..... Count 21
- 10676 *Feltia herilis* (Grt.)
July 22, 1988–Sep. 21, 1990..... Count 152
- 10891 *Ochropleura plecta* (L.)
May 18, 1988–Sep. 7, 1990..... Count 199
- 10903+ *Euagrotis illapsa* (Wlk.)
June 12, 1989–Aug. 30, 1991..... Count 3
- 10915 *Peridroma saucia* (Hbn.)
Aug. 21, 1989..... Count 1
- 10917 *Diarsia rubifera* (Grt.)
Aug. 3, 1990–Aug. 27, 1992..... Count 2
- 10942.1+ *Xestia dolosa* Franc.
May 30, 1991–Sep. 25, 1992..... Count 159
- 10943 *Xestia normaniana* (Grt.)
Aug. 14, 1989–Sep. 25, 1992..... Count 51
- 10944 *Xestia smithii* (Snell.)
Aug. 16, 1991–Sep. 25, 1992..... Count 90
- 10950+ *Xestia bicarnea* (Gn.)
Aug. 2–Sep. 13, 1991..... Count 194
- 10955 *Xestia badinodis* (Grt.)
Sep. 9, 1989–Sep. 25, 1992..... Count 5
- 10998 *Choephora fungorum* G. & R.
Sep. 2, 1989–Sep. 24, 1988..... Count 25
- 11006 *Protolampra brunneicollis* (Grt.)
June 26, 1989–Sep. 10, 1988..... Count 31
- 11007+ *Euerettagrotis sigmoides* (Gn.)
July 8–July 22, 1988..... Count 4
- 11010 *Heptagrotis phyllophora* (Grt.)
June 26–July 24, 1989..... Count 15
- 11012 *Cryptocala acadensis* (Bethune)
July 20, 1990..... Count 1
- 11029+ *Abagrotis alternata* (Grt.)
July 12, 1991–Sep. 25, 1992..... Count 34
- 11068 *Helicoverpa zea* (Boddie)
Sep. 9, 1989..... Count 1
- 11128 *Schinia arcigera* (Gn.)
Aug. 9, 1990..... Count 1

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CHECKLIST OF THE MOTHS OF GROVES WOODS PRESERVE, TRUMBULL COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Groves Woods Preserve in Trumbull County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988–1992) and includes 29,449 specimens representing 525 species. The study began in 1987 and continued through 1996, but only data for 1988–1992 are included here. The checklist is a historical record of the species that were present in 1988–1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after ten years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988–1992 is 6.81 and the Shannon-Wiener Evenness Index is 0.75. Two hundred twenty-one of the 525 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. Of the 221 Groves species which are widespread, 77 had counts of 10 or fewer at Groves. Four species of owl moths that were collected at Groves are of special interest in Ohio. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Introduction

The objective of this study was to document the population changes of native moths for ten years at several sites within the drainage basin of the Grand River in Trumbull, Ashtabula, and Lake Counties, Ohio, during gypsy moth invasion and control. This is the third in a series of six checklists that tabulate the moths collected at each site during 1988–1992.

Over this same period, the population of the gypsy moth increased in the entire drainage basin. Pheromone trap catches of male gypsy moths increased at Groves Woods Preserve from $50 \pm 16(2)$ per trap in 1987 [mean \pm standard error (number of traps)], to $51 \pm 18(4)$ in 1988, $256 \pm 35(3)$ in 1989, $137 \pm 16(4)$ in 1990, and $189 \pm 10(4)$ in 1991. Pheromone trapping was discontinued after 1991. Ultraviolet-light-trap catches of male gypsy moths also increased, from 1 in 1987, to 25 in 1988, 84 in 1989, 109 in 1990, 43 in 1991, and 90 in 1992, but noticeable defoliation was not observed at Groves Woods Preserve.

The overall study provides baseline data on pre-outbreak moth diversity, as well as data on the impact of gypsy moth control agents.

Description of the Surveillance Site at Groves Woods Preserve

Groves Woods, a preserve of The Cleveland Museum of Natural History, is composed of 62.7 ha of beech-maple mixed, hardwood forest (Bissell, 1998) and is bordered by Girdle Road on the west and Sweet Road on the north (Figure 1). Garden Creek transects the woods (Anonymous, 1995). The Preserve is situated on Hiram Till, ground moraine, and end moraine (White, 1982, p. 47, Pl. 1).

The light trap at Groves Woods was located in Mesopotamia Township in Trumbull County on Girdle Road at latitude $41^{\circ} 29' 04''$ N and longitude $80^{\circ} 58' 17''$ W (U.S. Geological Survey West Farmington, Ohio, 7.5-minute quadrangle topographic map; Figure 1).

Groves Woods is located approximately 22 km southeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

The composition of the canopy and understory was evaluated for the 2500 m^2 of forest centered on the surveillance trap (point-quarter technique, nine points;

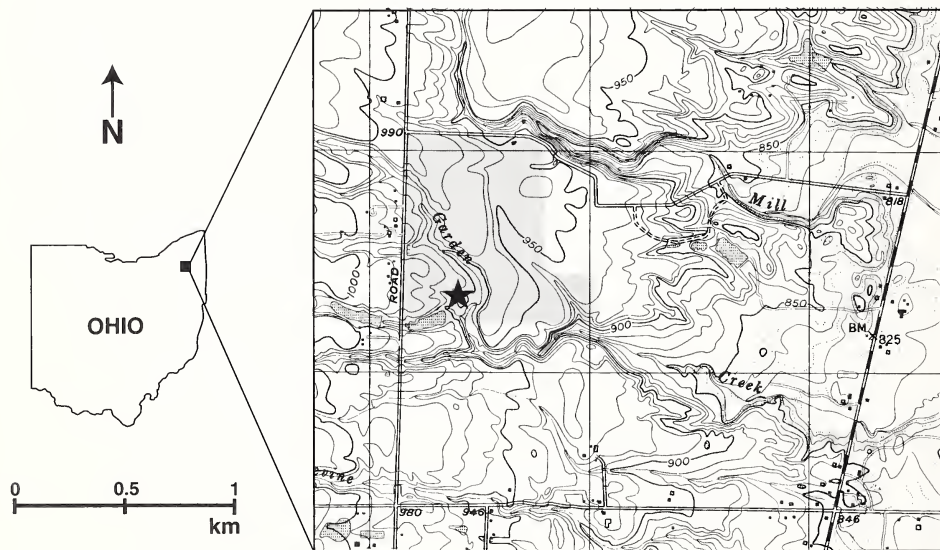


Figure 1. Map of the study area (adapted from the U.S. Geological Survey West Farmington, Ohio, 7.5-minute quadrangle topographic map). Shaded area delineates Groves Woods Preserve; star indicates position of surveillance trap within the Preserve.

Table 1. Importance values for trees at the surveillance site at Groves Woods. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Tree Species		Canopy	Understory
Oak, northern red	<i>Quercus rubra</i> L.	141	0
Maple, sugar	<i>Acer saccharum</i> Marsh	53	131
Beech, American	<i>Fagus grandifolia</i> Ehrh.	48	113
Maple, red	<i>Acer rubrum</i> L.	25	9
Oak, white	<i>Quercus alba</i> L.	25	9
Cherry, black	<i>Prunus serotina</i> Ehrh.	8	0
Hornbeam, American	<i>Carpinus caroliniana</i> Walt.	0	11
Dogwood, flowering	<i>Cornus florida</i> L.	0	10
Hop Hornbeam, eastern	<i>Ostrya virginiana</i> (Mill.) K. Koch	0	9
Rhododendron, domestic	<i>Rhododendron</i> sp.	0	8

Cottam and Curtis, 1956; Cox, 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90 m at Groves Woods. The importance values for the trees at the surveillance site at Groves Woods are given in Table 1.

The herbaceous plants and small shrubs included the spindle tree *Euonymus obovatus* Nutt. and blueberry *Vaccinium pallidum* Ait. (James K. Bissell, personal communication, 1998; author citations according to Kartesz, 1994). These species were selected from a longer list of Groves species on deposit in the Herbarium at The Cleveland Museum of Natural History. The surveillance trap was within 600 m of a pasture and within 300 m of a pond.

Surveillance Techniques

One Elliscope®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, from late May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were computerized. All the specimens collected are deposited in the Insect Collection at The Cleveland Museum of Natural History.

Results and Discussion

A total of 29,449 specimens representing 525 species were collected in 1988–1992 (Appendix). Species were

identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al. (1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodges et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 33 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1987 to 1996, is shown in Figure 2. In 1987 (not included in this checklist), 272 species were collected, and in 1996, after ten years, the total had reached 611 (1993–1996, also not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Groves Woods and five years would have been a minimum. The species accumulation curve was still rising after ten years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: fall, winter, and early spring moths are missing because collecting was not begun until the end of May and collecting ended in September. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

Relative abundances of the 525 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The Shannon-Wiener Diversity Index is 6.81 and the Shannon-Wiener Evenness Index is 0.75.

Over 13 percent of the total count was composed of lesser maple spanworm moth *Itame pustularia* (6273). The next most abundant species was American ermine

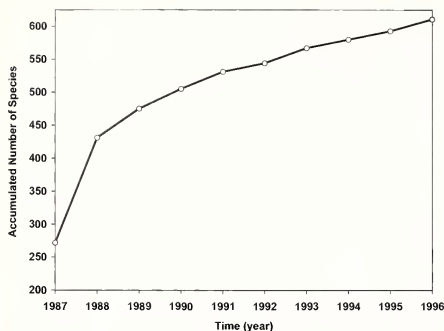


Figure 2. Plot of the annual accumulation of species collected at Groves Woods Preserve, 1987–1996.

moth *Yponomeuta multipunctella* (2420) whose larva feeds on euonymous. Following, in order of decreasing abundance, were: forest tent caterpillar moth *Malacosoma disstria* (7698) whose larva feeds on trees and shrubs, especially aspens and maples; sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants; greater black-letter dart *Xestia dolosa* (10942.1+) whose larva feeds on apple, clover, maples, etc.; agreeable tiger moth *Spilosoma congrua* (8134) whose larva feeds on herbaceous plants; banded tussock moth

Halysidota tessellaris (8203+) whose larva feeds on many deciduous trees; rotund idia *Idia rotundalis* (8326) whose larva feeds on dead coral fungus and dead leaves; disparaged arches *Polia detracta* (10288+) whose larva feeds on clover, blueberries, oaks, etc.; and leafroller moth *Choristoneura fractivittana* (3632) whose larva feeds on apple, beeches, birches, etc.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 221 Groves species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988; Krebs, 1994). Three explanations have been proposed (Krebs, 1994). First, the relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not exist, when abundance is viewed from the perspective of abundance at Groves. Of the 221 Groves species which are widespread in northeast Ohio, 77 had total counts of 10 or fewer at Groves.

Overall, there is a close correspondence between the

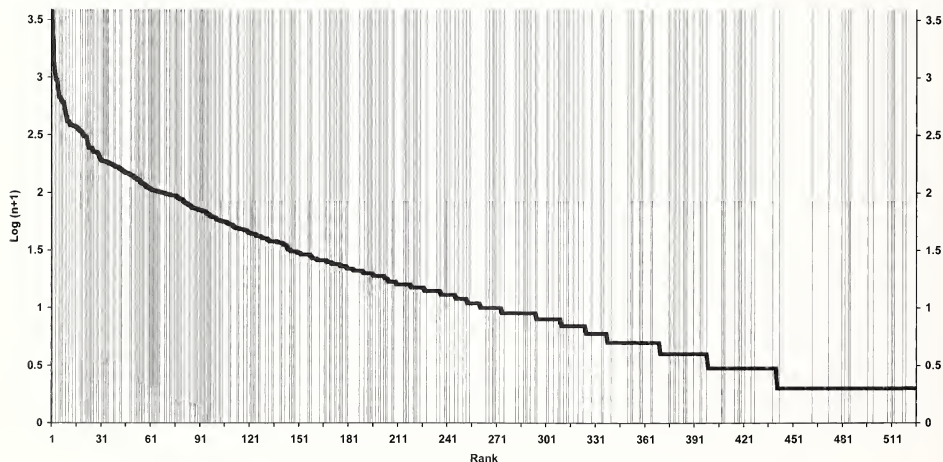


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Groves Woods Preserve, 1988–1992.

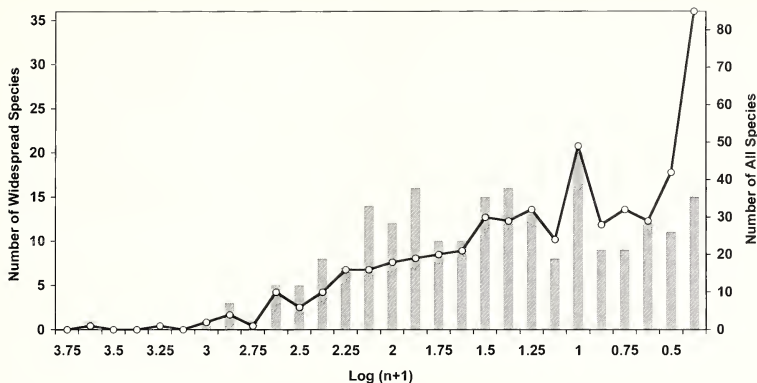


Figure 4. Correspondence between the total number of Groves species in an abundance interval (line, scale at right) and the number of widespread Groves species in the same abundance interval (bar, scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

number of widespread species in an abundance interval and the total number of species (Figure 4). Only the decrease in the proportion of widespread species in the singleton interval conforms to expectation. The 85 singleton species at Groves include only 15 widespread species whereas the 42 doubleton species include 11 widespread species.

Four species of owlet moths collected at Groves are listed as being of special interest in Rings et al. (1992): formosa looper moth *Chrysanypha formosa* (8904) whose larva feeds on blueberry and huckleberry; airy apamea *Apamea vultuosa* (9341) whose larva feeds on grasses; bridgham's brocade *Oligia bridghami* (9415) whose larval host is unrecorded; and scurfy quaker *Homorthodes fufurata* (10532) whose larva feeds on maples.

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Appendix. Checklist of species collected at Groves Woods Preserve, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection, and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family TINEIDAE

- 372+ *Acrolophus phumfrontella* (Clem.)
July 22, 1988 Count 1

Family OECOPHORIDAE

- 882 *Agonopterix robinella* (Pack.)
June 4–Aug. 21, 1989 Count 46
957 *Psilocorsis reflexella* Clem.
May 28, 1989–July 8, 1988 Count 20
1014+ *Antaeotricha leucitana* (Zell.)
May 18, 1988–Sep. 2, 1989 Count 246
1046 *Callima argenticinctella* Clem.
July 13–Aug. 3, 1990 Count 9

Family GELECHIIDAE

- 2295 *Trichotape flavocostella* (Clem.)
June 20, 1991–Aug. 3, 1990 Count 15

Family YPONOMEUTIDAE

- 2401 *Atteva punctella* (Cram.)
July 5, 1991 Count 1
2420 *Yponomeuta multipunctella* Clem.
June 13, 1991–Aug. 26, 1988 Count 1336

Family SESIIDAE

- 2554 *Synanthedon acerni* (Clem.)
July 22–Aug. 5, 1988 Count 2

Family TORTRICIDAE

- 3186 *Epiblema scudderiana* (Clem.)
June 1, 1988 Count 1
3361 *Ancylis semiovana* (Zell.)
June 1, 1988 Count 4
3494 *Melioscopus latiferreanus* (Wlsm.)
Aug. 14–Sep. 9, 1989 Count 5
3503 *Croesia semipurpurana* (Kft.)
June 15, 1988–July 4, 1989 Count 24
3504 *Croesia curvalana* (Kft.)
June 26, 1989 Count 3
3594 *Pandemis limitata* (Rob.)
June 1, 1988–Sep. 14, 1990 Count 24
3597 *Argyrotaenia velutinana* (Wlk.)
July 29, 1988 Count 28
3623 *Argyrotaenia quercifoliaria* (Fitch)
June 6, 1991–July 24, 1992 Count 23
3624 *Argyrotaenia alisellana* (Rob.)
June 15, 1990–June 20, 1991 Count 2
3625 *Argyrotaenia mariana* (Fern.)
May 18, 1988 Count 1
3632 *Choristoneura fractivittana* (Clem.)
June 1, 1990–July 4, 1989 Count 414

- 3633 *Choristoneura parallela* (Rob.)
July 10, 1989–Aug. 31, 1990 Count 12
3635 *Choristoneura rosaceana* (Harr.)
June 12, 1989–Sep. 14, 1990 Count 37
3648 *Archips argyrospila* (Wlk.)
June 22–July 13, 1990 Count 13
3686 *Clepsis melaleucana* (Wlk.)
June 1, 1988–June 26, 1989 Count 36
3720 *Sparganothis reticulatana* (Clem.)
June 26–Aug. 21, 1989 Count 4
3725 *Sparganothis petitiiana* (Rob.)
June 29, 1990–July 31, 1989 Count 11
3748 *Amorbia humerosana* Clem.
June 1, 1988 Count 1

Family LIMACODIDAE

- 4652 *Tortricidia testacea* Pack.
June 1, 1988–June 26, 1989 Count 94
4654 *Tortricidia flexuosa* (Grt.)
June 6, 1991–July 22, 1988 Count 100
4659 *Packardia geminata* (Pack.)
June 1–July 15, 1988 Count 13
4661 *Packardia elegans* (Pack.)
June 6, 1991–July 13, 1990 Count 14
4665 *Lithacodes fasciola* (H.-S.)
June 27, 1991–July 29, 1988 Count 39
4667 *Apoda y-inversum* (Pack.)
June 15, 1988–July 24, 1989 Count 10
4669 *Apoda biguttata* (Pack.)
June 15–June 22, 1988 Count 8
4671 *Prolinacodes badia* (Hbn.)
June 27, 1991–July 20, 1990 Count 8
4681 *Isa textula* (H.-S.)
June 6, 1991–July 10, 1989 Count 5
4685 *Adoneta spinuloides* (H.-S.)
June 22, 1988–July 20, 1990 Count 8
4697 *Euclea delphinii* (Bdv.)
June 19, 1989–July 8, 1988 Count 11

Family CRAMBIDAE

- 4703 *Gesneria centuriella* (D. & S.)
June 1, 1988–Aug. 21, 1989 Count 223
4748 *Munroessa icciusalis* (Wlk.)
June 1, 1988–Sep. 9, 1989 Count 16
4751 *Munroessa gyralis* (Hulst)
June 8, 1990–Sep. 9, 1989 Count 3
4889 *Dicynolomia julianalis* (Wlk.)
June 26, 1989–July 15, 1988 Count 8
4897 *Evergestis pallidata* (Hufn.)
June 5, 1992–Sep. 13, 1991 Count 55

4936	<i>Saucrobotys futilalis</i> (Led.) Aug. 2, 1991	Count 3
4937	<i>Nascia acutella</i> (Wlk.) July 10, 1989	Count 1
4944	<i>Crociodophoda serratissimalis</i> Zell. June 13, 1991–Sep. 2, 1989	Count 197
4945	<i>Crociodophora tuberculalis</i> Led. June 20, 1991–Aug. 7, 1992	Count 28
4949	<i>Ostrinia nubilalis</i> (Hbn.) June 1, 1988–Sep. 13, 1991	Count 102
4950	<i>Fumiborys fumalis</i> (Gn.) July 29, 1988–Sep. 4, 1992	Count 6
4953a	<i>Phlyctaenia coronata tertialis</i> (Gn.) June 5–Sep. 4, 1992	Count 15
4962	<i>Hahncappsia marculenta</i> (G. & R.) June 1–Aug. 26, 1988	Count 13
5040	<i>Pyrausta bicoloralis</i> (Gn.) June 6, 1991–Aug. 24, 1990	Count 18
5071	<i>Pyrausta acronialis</i> (Wlk.) June 6–Sep. 21, 1991	Count 8
5079	<i>Udea rubigalis</i> (Gn.) June 4, 1989–Sep. 25, 1992	Count 153
5142	<i>Diacme elealis</i> (Wlk.) June 20, 1991–Aug. 21, 1992	Count 94
5156	<i>Nomophila nearctica</i> Mun. June 4–Sep. 9, 1989	Count 12
5159	<i>Desmia funeralis</i> (Hbn.) June 19–Sep. 9, 1989	Count 43
5160	<i>Desmia maculalis</i> Westwood July 12, 1991–Aug. 9, 1990	Count 2
5182	<i>Blepharomastix ranalis</i> (Gn.) June 26, 1989–July 24, 1988	Count 4
5226	<i>Palpita magniferalis</i> (Wlk.) June 1, 1988–Aug. 23, 1991	Count 79
5228	<i>Polygrammodes flavidalis</i> (Gn.) June 20, 1991–Aug. 26, 1988	Count 70
5229	<i>Polygrammodes langdonalis</i> (Grt.) July 8, 1988	Count 2
5241	<i>Pantographa limata</i> (G. & R.) June 20, 1991–Sep. 4, 1992	Count 188
5272	<i>Herpetogramma bipunctalis</i> (F.) June 22, 1988–Aug. 21, 1989	Count 35
5275	<i>Herpetogramma pterextalis</i> (Led.) July 10–Aug. 21, 1989	Count 41
5280	<i>Herpetogramma aeglealis</i> (Wlk.) July 3, 1992–Aug. 2, 1991	Count 57
5281	<i>Pilocrocis ramentalis</i> Led. July 22, 1988	Count 1
5362+	<i>Crambus agitatellus</i> Clem. June 1–Sep. 24, 1988	Count 922
5392	<i>Arequipa turbatella</i> Wlk. Aug. 7, 1992	Count 1
5403	<i>Agriphila vulgivaella</i> (Clem.) Aug. 23, 1991–Sep. 4, 1992	Count 4
5464	<i>Urola nivalis</i> (Drury) June 15, 1990–Aug. 7, 1992	Count 61
5465	<i>Vaxi auratella</i> (Clem.) July 15, 1988–July 27, 1990	Count 5
5466	<i>Vaxi critica</i> (Fbs.) July 22, 1988	Count 1

Family PYRALIDAE

5517	<i>Aglossa caprealis</i> (Hbn.) July 5, 1991	Count 2
5518	<i>Aglossa cuprina</i> Zell. June 6, 1991–Aug. 31, 1990	Count 177
5524	<i>Hypsopygia costalis</i> (F.) June 22–July 22, 1988	Count 21
5532	<i>Herculia infimbrialis</i> Dyar July 13, 1990–July 31, 1989	Count 3
5552	<i>Galasa nigrinodis</i> (Zell.) July 4, 1989–July 5, 1991	Count 2
5556	<i>Tosale oviplagalis</i> (Wlk.) June 19, 1989–July 27, 1990	Count 28
5571	<i>Condylolomia participalis</i> Grt. June 13, 1991–July 20, 1990	Count 140
5577	<i>Epipaschia superatalis</i> Clem. June 27, 1991–July 10, 1989	Count 4
5606	<i>Tetralopha asperatella</i> (Clem.) June 29–Aug. 9, 1990	Count 4
5622	<i>Galleria mellonella</i> (L.) Sep. 13, 1991	Count 1
5997	<i>Euzophora ostricologrella</i> Hulst July 8, 1988–Aug. 3, 1990	Count 4
6053	<i>Peoria approximella</i> (Wlk.) June 12, 1992–July 15, 1988	Count 9

Family THYRIDIDAE

6079	<i>Dysodia granulata</i> (Neum.) June 26–Aug. 21, 1989	Count 8
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Family THYATRIDAE

6235	<i>Habrosyne scripta</i> (Gosse) May 30, 1991–June 15, 1988	Count 3
6237	<i>Pseudothyatira cymatophoroides</i> (Gn.) June 26, 1989–Aug. 5, 1988	Count 7

Family DREPANIDAE

6251	<i>Drepana arcuata</i> Wlk. June 15, 1988	Count 2
6255	<i>Oreta rosea</i> (Wlk.) May 30, 1991–Aug. 31, 1990	Count 6

Family GEOMETRIDAE

6261	<i>Helionota cycladata</i> G. & R. June 15–June 22, 1988	Count 3
6270	<i>Protitame virginialis</i> (Hulst) July 19, 1991–Aug. 5, 1988	Count 2
6272	<i>Eumacaria latiferrugata</i> (Wlk.) July 19, 1991	Count 1
6273	<i>Itame pustularia</i> (Gn.) June 13–Sep. 21, 1991	Count 3897
6299	<i>Itame coortaria</i> (Hulst) May 18, 1988–July 17, 1992	Count 20
6303	<i>Itame subcessaria</i> (Wlk.) June 27, 1991–July 15, 1988	Count 8
6335+	<i>Semiothisa acquiferaria</i> (Wlk.) May 18, 1988–Sep. 9, 1988	Count 104
6342	<i>Semiothisa bisignata</i> (Wlk.) July 4, 1989–July 15, 1988	Count 6
6344+	<i>Semiothisa signaria</i> (Hbn.) May 28, 1992–Sep. 9, 1989	Count 76

6386	<i>Semiothisa ocellinata</i> (Gn.) June 27, 1991–Aug. 19, 1988	Count 25	6823	<i>Metarranthis angularia</i> B. & McD. June 8–June 22, 1988	Count 4
6405	<i>Semiothisa gnophosaria</i> (Gn.) June 22–Aug. 24, 1990	Count 21	6825	<i>Metarranthis indeclinata</i> (Wlk.) May 28–June 19, 1992	Count 13
6583	<i>Anacamptodes ephyriaria</i> (Wlk.) June 27, 1991–July 24, 1989	Count 44	6826	<i>Metarranthis hypocharia</i> (H.-S.) May 30, 1991–June 26, 1989	Count 88
6584	<i>Anacamptodes humaria</i> (Gn.) July 5–Aug. 23, 1991	Count 4	6827	<i>Metarranthis refractaria</i> (Gn.) June 12–July 3, 1992	Count 4
6586	<i>Anacamptodes defectaria</i> (Gn.) July 13, 1990	Count 1	6834	<i>Cepphis decoloraria</i> (Hulst) June 19, 1989–July 8, 1988	Count 3
6588	<i>Iridopsis larvaria</i> (Gn.) May 30, 1991–Aug. 24, 1990	Count 56	6835	<i>Cepphis armataria</i> (H.-S.) June 13, 1991–July 8, 1988	Count 4
6590	<i>Anavitrinella pampinaria</i> (Gn.) May 30, 1991–Sep. 24, 1988	Count 70	6836	<i>Anagoga occiduaris</i> (Wlk.) May 18, 1988–Aug. 9, 1990	Count 10
6597	<i>Ectropis crepuscularia</i> (D. & S.) June 13, 1991–Sep. 14, 1990	Count 120	6838+	<i>Probole amicaria</i> (H.-S.) May 21, 1989–Aug. 16, 1990	Count 132
6598	<i>Protoboarmia porcellaria</i> (Gn.) June 6–Sep. 13, 1991	Count 31	6839	<i>Probole nepiasaria</i> (Wlk.) July 12, 1991	Count 1
6599	<i>Epimecis hortaria</i> (F.) May 18, 1988–July 27, 1990	Count 43	6840	<i>Plagodis serinaria</i> H.-S. May 18–June 22, 1988	Count 186
6620+	<i>Melanolophia canadaria</i> (Gn.) May 18, 1988–Sep. 21, 1991	Count 225	6841	<i>Plagodis kuetzingi</i> (Grt.) June 4, 1989–July 19, 1991	Count 6
6638	<i>Eufidonia notataria</i> (Wlk.) June 4, 1989–June 5, 1992	Count 2	6842	<i>Plagodis phlogosaria</i> (Gn.) July 8, 1988–July 24, 1989	Count 8
6640a	<i>Biston betularia cognataria</i> (Gn.) June 26, 1989–Aug. 2, 1991	Count 5	6843	<i>Plagodis fervidaria</i> (H.-S.) July 12, 1991–Aug. 21, 1989	Count 4
6654	<i>Hypagyrtis unipunctata</i> (Haw.) June 5, 1992–Aug. 24, 1990	Count 39	6844	<i>Plagodis alcoolaria</i> (Gn.) May 18, 1988–Aug. 2, 1991	Count 110
6655	<i>Hypagyrtis esther</i> (Barnes) May 30, 1991–Sep. 14, 1990	Count 310	6863	<i>Caripeta divisata</i> Wlk. June 29, 1990–Aug. 16, 1991	Count 20
6667	<i>Lomographa vestaliata</i> (Gn.) May 28, 1992–June 29, 1990	Count 117	6884	<i>Besma endropiaria</i> (G. & R.) May 28, 1992–Aug. 24, 1990	Count 96
6677	<i>Cabera erythemaria</i> Gn. May 30, 1991–Sep. 2, 1989	Count 73	6885	<i>Besma quercivoraria</i> (Gn.) May 18, 1988–Aug. 24, 1990	Count 48
6678	<i>Cabera variolaria</i> Gn. May 30, 1991–Aug. 14, 1989	Count 7	6892	<i>Lambdina pellucidaria</i> (G. & R.) May 18, 1988	Count 2
6720	<i>Lyttosia unitaria</i> (H.-S.) June 6, 1991–July 10, 1989	Count 50	6906	<i>Nepytia canosaria</i> (Wlk.) Sep. 25, 1992	Count 1
6724	<i>Euchlaena serrata</i> (Drury) July 3, 1992–July 20, 1990	Count 7	6912	<i>Sicya macularia</i> (Harr.) June 22, 1988–July 10, 1992	Count 16
6725	<i>Euchlaena mucaria</i> (Wlk.) May 30, 1991–July 4, 1989	Count 26	6941	<i>Eusarca confusaria</i> Hbn. June 12, 1989–Sep. 10, 1992	Count 37
6729	<i>Euchlaena johnsonaria</i> (Fitch) June 12, 1989–Aug. 26, 1988	Count 3	6963	<i>Tetracis crocallata</i> Gn. June 15–July 8, 1988	Count 8
6737	<i>Euchlaena tigrinaria</i> (Gn.) Aug. 5–Aug. 19, 1988	Count 2	6964	<i>Tetracis cachexiata</i> Gn. May 18, 1988–Aug. 23, 1991	Count 244
6739	<i>Euchlaena irroraria</i> (B. & McD.) May 30, 1991–June 19, 1989	Count 5	6965	<i>Eugonobapta nivosaria</i> (Gn.) June 13–Sep. 13, 1991	Count 167
6740+	<i>Xanthotype urticaria</i> Swett May 30, 1991–Aug. 24, 1990	Count 22	6966	<i>Eutrapela clemataria</i> (J.E. Smith) May 18, 1988–Sep. 14, 1990	Count 101
6753+	<i>Pero honestaria</i> (Wlk.) May 21–Sep. 2, 1989	Count 128	6982	<i>Prochoerodes transversata</i> (Drury) June 20, 1991–Sep. 25, 1992	Count 107
6796	<i>Campaea perlata</i> (Gn.) May 30, 1991–Sep. 24, 1988	Count 382	6987	<i>Antepione thisoaria</i> (Gn.) June 1, 1990–Aug. 14, 1989	Count 12
6798	<i>Ennomos subsignaria</i> (Hbn.) June 20, 1991–Aug. 21, 1992	Count 167	7009	<i>Nematocampa limbata</i> (Haw.) June 20, 1991–Sep. 7, 1990	Count 55
6819	<i>Metanema inatomaria</i> Gn. June 1, 1988–Aug. 24, 1990	Count 4			
6822	<i>Metarranthis duaria</i> (Gn.) June 15, 1988	Count 1			

7033	<i>Nemoria lixaria</i> (Gn.) June 8, 1988.	Count 1
7046+	<i>Nemoria bistriaria</i> Hbn. May 28, 1989–Aug. 27, 1992.	Count 37
7047	<i>Nemoria rubrifrontaria</i> (Pack.) June 1, 1988.	Count 1
7048	<i>Nemoria minusaria</i> (Gn.) May 28, 1992–June 19, 1989.	Count 7
7053	<i>Dichorda iridaria</i> (Gn.) June 4, 1989–July 31, 1992.	Count 6
7058	<i>Synchlora aerata</i> (F.) May 30–Aug. 30, 1991.	Count 13
7071	<i>Chlorochlamys chloroleucaria</i> (Gn.) June 1–July 8, 1988.	Count 2
7084	<i>Hethemia pistasciaria</i> (Gn.) June 22, 1988.	Count 1
7132	<i>Pleuroprucha insulsaria</i> (Gn.) June 20, 1991–Sep. 9, 1989.	Count 47
7136	<i>Cyclophora packardii</i> (Proust) May 30, 1991–Sep. 10, 1988.	Count 26
7139	<i>Cyclophora pendulinaria</i> (Gn.) Aug. 2, 1991.	Count 2
7146	<i>Haematopsis grataria</i> (F.) June 27, 1991–Sep. 9, 1989.	Count 6
7157	<i>Scopula cacuminiaria</i> (Morr.) June 12, 1989–Aug. 2, 1991.	Count 2
7159	<i>Scopula limboundata</i> (Haw.) June 20–Sep. 13, 1991.	Count 181
7165	<i>Scopula quadrilineata</i> (Pack.) Aug. 7, 1992.	Count 1
7169	<i>Scopula inductata</i> (Gn.) May 30, 1991–Aug. 16, 1990.	Count 4
7189	<i>Dysstroma hersiliata</i> (Gn.) June 12, 1989–July 8, 1988.	Count 9
7196+	<i>Eulithis diversilineata</i> (Hbn.) June 27, 1991–Sep. 25, 1992.	Count 90
7284	<i>Eutrepisia inconstans</i> (Gey.) July 15, 1988.	Count 10
7307	<i>Mesoleuca ruficollata</i> (Gn.) June 5, 1992–Sep. 9, 1989.	Count 4
7329	<i>Anticlea vasilata</i> Gn. May 18, 1988.	Count 1
7333	<i>Stannodes gibbicostata</i> (Wlk.) Sep. 10, 1988.	Count 1
7368	<i>Xanthorhoe labradorensis</i> (Pack.) Aug. 2, 1991–Sep. 14, 1990.	Count 29
7371	<i>Xanthorhoe iduata</i> (Gn.) June 12–Sep. 4, 1992.	Count 2
7388	<i>Xanthorhoe ferrugata</i> (Cl.) June 20, 1991–Sep. 9, 1989.	Count 6
7390	<i>Xanthorhoe lacustrata</i> (Gn.) June 5, 1992–Sep. 7, 1990.	Count 38
7394	<i>Epirrhoe alternata</i> (Muller) June 1, 1990–Sep. 9, 1989.	Count 8
7399a	<i>Euphyia unangulata intermediata</i> (Gn.) June 6, 1991–Sep. 2, 1989.	Count 18
7414	<i>Orthonama obstipata</i> (F.) May 30–Sep. 6, 1991.	Count 99

7416	<i>Orthonama centrostrigaria</i> (Woll.) May 30, 1991–Sep. 14, 1990.	Count 338
7422	<i>Hydrelia inornata</i> (Hulst) May 30–Aug. 16, 1991.	Count 13
7423	<i>Hydrelia albifera</i> (Wlk.) June 6, 1991–Aug. 21, 1992.	Count 15
7430	<i>Trichodezia albiovittata</i> (Gn.) July 12, 1991.	Count 1
7440	<i>Eubaphe mendica</i> (Wlk.) May 30, 1991–Aug. 27, 1992.	Count 184
7445	<i>Horisme intestinata</i> (Gn.) June 6, 1991–Sep. 2, 1989.	Count 15
7474+	<i>Eupithecia miserulata</i> Grt. May 18, 1988–Sep. 25, 1992.	Count 380
7640	<i>Lobophora nivigerata</i> Wlk. June 4, 1989.	Count 1
7645	<i>Heterophleps refusaria</i> (Wlk.) June 8, 1988.	Count 2
7647	<i>Heterophleps triguttaria</i> H.-S. June 5, 1992–Aug. 19, 1988.	Count 17
7648	<i>Dyspteris abortivaria</i> (H.-S.) June 15, 1988.	Count 1

Family APATELODIDAE

7663	<i>Apatelodes torrefacta</i> (J.E. Smith) June 19, 1989–July 24, 1992.	Count 14
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Family LASIOCAMPIDAE

7670	<i>Tolyte velleda</i> (Stoll) Sep. 7, 1990–Sep. 25, 1992.	Count 20
7673	<i>Tolyte laricis</i> (Fitch) July 12, 1991–Sep. 9, 1989.	Count 13
7698	<i>Malacosoma distria</i> Hbn. June 13, 1991–July 24, 1989.	Count 975
7701	<i>Malacosoma americanum</i> (F.) June 13, 1991–July 24, 1989.	Count 62

Family SATURNIIDAE

7715	<i>Dryocampa rubicunda</i> (F.) June 1–July 29, 1988.	Count 36
7746	<i>Automeris io</i> (F.) May 30, 1991–July 8, 1988.	Count 14
7757	<i>Antheraea polyphemus</i> (Cram.) June 6, 1991–July 29, 1988.	Count 12
7758	<i>Actias luna</i> (L.) May 28, 1989–July 15, 1988.	Count 15
7764	<i>Callosamia promethea</i> (Drury) May 30–June 27, 1991.	Count 2
7765	<i>Callosamia angulifera</i> (Wlk.) July 15, 1988.	Count 2
7767	<i>Hyalophora cecropia</i> (L.) June 1, 1990.	Count 1

Family SPHINGIDAE

7821	<i>Smerinthus jamaicensis</i> (Drury) June 4, 1989–July 26, 1991.	Count 2
7824	<i>Paonias excaecatus</i> (J.E. Smith) May 30, 1991–Aug. 5, 1988.	Count 60
7825	<i>Paonias myops</i> (J.E. Smith) May 30, 1991–July 29, 1988.	Count 15

7827	<i>Laotloe juglandis</i> (J.E. Smith)	
	May 28, 1992–July 17, 1989	Count 18
7828	<i>Pachysphinx modesta</i> (Harr.)	
	June 1, 1988	Count 1
7870	<i>Sphecodina abbottii</i> (Swainson)	
	June 1, 1988	Count 1
7871	<i>Deidamia inscripta</i> (Harr.)	
	May 28, 1992	Count 2

Family NOTODONTIDAE

7895	<i>Clostera albosigma</i> Fitch	
	June 22, 1988–Aug. 21, 1989	Count 3
7898	<i>Clostera strigosa</i> (Grt.)	
	June 1, 1988–Aug. 2, 1991	Count 7
7901	<i>Clostera apicalis</i> (Wlk.)	
	June 1, 1990–Aug. 21, 1989	Count 9
7902	<i>Datana ministra</i> (Drury)	
	July 15, 1988–July 24, 1989	Count 18
7903	<i>Datana angusii</i> G. & R.	
	June 1, 1990–July 24, 1989	Count 19
7906+	<i>Datana contracta</i> Wlk.	
	May 30, 1991–July 29, 1988	Count 22
7915	<i>Nadatra gibbosa</i> (J.E. Smith)	
	May 21, 1989–Aug. 24, 1990	Count 334
7919	<i>Peridea basitriens</i> (Wlk.)	
	May 30, 1991–Aug. 21, 1989	Count 127
7920	<i>Peridea angulosa</i> (J.E. Smith)	
	May 30, 1991–Sep. 9, 1989	Count 173
7922	<i>Pheosia rimosa</i> Pack.	
	June 27, 1991–Aug. 16, 1990	Count 8
7929	<i>Nerice bidentata</i> Wlk.	
	May 21, 1989–Aug. 24, 1990	Count 18
7930	<i>Ellida caniplaga</i> (Wlk.)	
	June 27, 1991–July 13, 1990	Count 6
7931	<i>Gluphisia septentrionis</i> Wlk.	
	June 22–July 29, 1988	Count 3
7936	<i>Furcula borealis</i> (Guer.-Meneville)	
	July 12, 1991–Aug. 16, 1990	Count 2
7939	<i>Furcula occidentalis</i> (Lint.)	
	July 29, 1988	Count 1
7951+	<i>Symmerista albifrons</i> (J.E. Smith)	
	May 30, 1991–Aug. 16, 1990	Count 93
7957	<i>Dasytophia anguina</i> (J.E. Smith)	
	Aug. 7, 1989	Count 1
7958	<i>Dasytophia thyatiroides</i> (Wlk.)	
	May 30, 1991–Aug. 16, 1990	Count 25
7975	<i>Macrurocampa marthesia</i> (Cram.)	
	June 20, 1991–Aug. 9, 1990	Count 169
7994	<i>Heterocampa guttivitta</i> (Wlk.)	
	May 21, 1989–July 15, 1988	Count 241
7995	<i>Heterocampa biundata</i> Wlk.	
	July 26, 1991–Aug. 9, 1990	Count 3
7998	<i>Lochnaeus manteo</i> Doubleday	
	June 1, 1990–Aug. 5, 1988	Count 31
7999	<i>Lochnaeus bilineata</i> (Pack.)	
	June 5, 1992–Aug. 24, 1990	Count 23
8005	<i>Schizura ipomoeae</i> Doubleday	
	June 5–Aug. 7, 1992	Count 4

8007	<i>Schizura unicoloris</i> (J.E. Smith)	
	May 30, 1991–Aug. 31, 1990	Count 57
8011	<i>Schizura leptinoides</i> (Grt.)	
	May 30, 1991–Aug. 21, 1989	Count 27
8012	<i>Oligocentria semirufescens</i> (Wlk.)	
	June 15–July 20, 1990	Count 7
8017	<i>Oligocentria lignicolor</i> (Wlk.)	
	June 15, 1990–Aug. 16, 1991	Count 14

Family ARCTIIDAE

8045.1	<i>Crambidia pallida</i> Pack.	
	July 22, 1988–Sep. 7, 1990	Count 37
8090	<i>Hypoprepia fucosa</i> Hbn.	
	July 12, 1991	Count 1
8104	<i>Comachara cadburyi</i> Franc.	
	June 5, 1992	Count 1
8107	<i>Haploa clymene</i> (Brown)	
	July 5, 1991–July 31, 1992	Count 9
8121+	<i>Holometina aurantiaca</i> (Hbn.)	
	May 30, 1991–Aug. 21, 1992	Count 366
8129	<i>Pyrrharetia isabella</i> (J.E. Smith)	
	May 30, 1991–Sep. 9, 1989	Count 41
8131	<i>Estigmene acrea</i> (Drury)	
	June 26, 1989	Count 1
8133	<i>Spilosoma latipennis</i> Stretch	
	May 30–Sep. 13, 1991	Count 112
8134	<i>Spilosoma congrua</i> Wlk.	
	May 21, 1989–July 17, 1992	Count 659
8137	<i>Spilosoma virginica</i> (F.)	
	May 28, 1989–Aug. 26, 1988	Count 60
8140	<i>Hyphantria cunea</i> (Drury)	
	May 30, 1991–July 10, 1992	Count 3
8156	<i>Phragmatobia fuliginosa</i> (L.)	
	July 31, 1989–Aug. 9, 1990	Count 2
8169+	<i>Apantesis phalerata</i> (Harr.)	
	May 28, 1992–Sep. 10, 1988	Count 102
8203+	<i>Halysidota tessellaris</i> (J.E. Smith)	
	June 6–Sep. 13, 1991	Count 611
8211	<i>Lophocampa caryae</i> Harr.	
	June 1, 1988–Sep. 4, 1992	Count 104
8230	<i>Cycnia tenera</i> Hbn.	
	June 20, 1991–Aug. 19, 1988	Count 7
8231	<i>Cycnia oregonensis</i> (Stretch)	
	June 1, 1990–Aug. 5, 1988	Count 6
8238	<i>Euchaetes egle</i> (Drury)	
	June 6, 1991–July 13, 1990	Count 10
8267	<i>Ciseps fulvicollis</i> (Hbn.)	
	May 30–Sep. 13, 1991	Count 44

Family LYMANTRIIDAE

8296	<i>Dasychira basiflava</i> (Pack.)	
	June 27, 1991–July 31, 1992	Count 22
8302	<i>Dasychira obliquata</i> (G. & R.)	
	July 26, 1991–Aug. 21, 1989	Count 2
8314	<i>Orgyia definita</i> Pack.	
	July 8, 1988–Sep. 14, 1990	Count 10
8316	<i>Orgyia leucostigma</i> (J.E. Smith)	
	June 20–Sep. 13, 1991	Count 4

- 8318 *Lymantria dispar* (L.)
July 5, 1991–Sep. 4, 1992 Count 351

Family NOCTUIDAE

- 8322 *Idia americalis* (Gn.)
May 30, 1991–Sep. 25, 1992 Count 68
- 8323+ *Idia aemula* Hbn.
June 6, 1991–Sep. 21, 1990 Count 160
- 8326 *Idia rotundalis* (Wlk.)
June 27, 1991–Sep. 4, 1992 Count 601
- 8327 *Idia forbesi* (French)
June 27, 1991–Aug. 21, 1992 Count 150
- 8329 *Idia diminuendis* (B. & McD.)
June 27, 1991–Aug. 27, 1992 Count 176
- 8330 *Idia scobialis* (Grt.)
July 13–Aug. 16, 1990 Count 28
- 8333 *Idia denticulalis* (Harv.)
July 8, 1988–Sep. 7, 1990 Count 10
- 8334 *Idia lubricalis* (Gey.)
July 4–Sep. 9, 1989 Count 77
- 8338 *Phalaenophana pyramusalis* (Wlk.)
June 1–Sep. 10, 1988 Count 9
- 8340 *Zanclognatha lituralis* (Hbn.)
June 6, 1991–Aug. 24, 1990 Count 40
- 8345 *Zanclognatha laevigata* (Grt.)
July 8, 1988–Sep. 9, 1989 Count 86
- 8347 *Zanclognatha obscuripennis* (Grt.)
Sep. 13, 1991 Count 1
- 8348 *Zanclognatha pedipalis* (Gn.)
June 12–Aug. 21, 1989 Count 5
- 8349 *Zanclognatha protamnusalis* (Wlk.)
July 5, 1991–Aug. 16, 1990 Count 10
- 8351 *Zanclognatha cruralis* (Gn.)
June 26, 1989–Aug. 9, 1990 Count 12
- 8352+ *Zanclognatha jachusalis* (Wlk.)
June 19, 1989–Sep. 21, 1990 Count 383
- 8355 *Chytolita morbidalis* (Gn.)
June 1–July 22, 1988 Count 64
- 8356 *Chytolita petrealis* Grt.
June 20, 1991–July 24, 1992 Count 11
- 8357 *Macrochilo absorptalis* (Wlk.)
June 22, 1988 Count 2
- 8357.1 *Macrochilo hypocritalis* Fgn.
July 10, 1989–Aug. 27, 1992 Count 4
- 8358 *Macrochilo litophora* (Grt.)
June 20, 1991–Aug. 5, 1988 Count 19
- 8362 *Phalaenostola metonalis* (Wlk.)
May 30, 1991–Aug. 26, 1988 Count 20
- 8363 *Phalaenostola emmelusalis* (Wlk.)
June 27, 1991–Sep. 7, 1990 Count 5
- 8364 *Phalaenostola larentioides* Grt.
July 5–Aug. 2, 1991 Count 6
- 8366 *Tetanolia mynesalis* (Wlk.)
July 5, 1991 Count 1
- 8368 *Tetanolia floridana* (Sm.)
Aug. 2, 1991 Count 1
- 8370 *Bleptina caradrinalis* Gn.
June 22–Aug. 3, 1990 Count 21

- 8378 *Renia salusalis* (Wlk.)
July 5, 1991–July 17, 1992 Count 3
- 8379 *Renia factiosalis* (Wlk.)
July 12, 1991–Sep. 4, 1992 Count 147
- 8381 *Renia discoloralis* Gn.
July 12, 1991–Sep. 9, 1989 Count 54
- 8384.1 *Renia flavipunctalis* (Gey.)
July 31, 1989 Count 1
- 8386 *Renia adspersigillus* (Bosc)
June 22, 1988–Aug. 21, 1992 Count 8
- 8387 *Renia sobrialis* (Wlk.)
June 20, 1991–July 31, 1989 Count 9
- 8393 *Lascoria ambigualis* Wlk.
June 22, 1988–July 27, 1990 Count 7
- 8397 *Palthis angularis* (Hbn.)
June 1, 1988–Sep. 9, 1989 Count 23
- 8398 *Palthis asopialis* (Gn.)
May 30, 1991–Sep. 21, 1990 Count 52
- 8401 *Redectis vitrea* (Grt.)
Sep. 9, 1989 Count 1
- 8404 *Rivula propinquialis* Gn.
May 30, 1991–Aug. 24, 1990 Count 47
- 8412 *Melanomna auricinctaria* Grt.
May 30, 1991–Aug. 24, 1990 Count 8
- 8420 *Hypenodes caducus* (Dyar)
July 5, 1991 Count 1
- 8421 *Hypenodes fractilinea* (Sm.)
May 30, 1991–Sep. 4, 1992 Count 147
- 8426 *Dyspyralis illocata* Warr.
July 12, 1991–July 27, 1990 Count 14
- 8427 *Dyspyralis puncticosta* (Sm.)
July 5, 1991–Aug. 27, 1992 Count 39
- 8428 *Dyspyralis nigella* (Stkr.)
July 12, 1991–Aug. 21, 1992 Count 20
- 8441 *Bomolocha manalis* (Wlk.)
June 15, 1990–Sep. 9, 1989 Count 18
- 8442 *Bomolocha baltimoralis* (Gn.)
June 1, 1990–Sep. 10, 1992 Count 72
- 8443 *Bomolocha bijugalis* (Wlk.)
July 12–July 26, 1991 Count 2
- 8444 *Bomolocha palparia* (Wlk.)
June 15, 1988–Aug. 24, 1990 Count 11
- 8445 *Bomolocha abalienalis* (Wlk.)
July 8, 1988–Aug. 21, 1992 Count 11
- 8446 *Bomolocha deceptalis* (Wlk.)
June 6, 1991–Sep. 7, 1990 Count 9
- 8447 *Bomolocha madefactalis* (Gn.)
June 22, 1988–Sep. 7, 1990 Count 8
- 8448 *Bomolocha sordidula* (Grt.)
June 22, 1988–Sep. 9, 1989 Count 3
- 8452 *Bomolocha edictalis* (Wlk.)
Aug. 3, 1990–Aug. 16, 1991 Count 4
- 8465 *Plathypena scabra* (F.)
June 6, 1991–Sep. 24, 1988 Count 68
- 8479 *Spargaloma sexpunctata* Grt.
May 30, 1991–Aug. 21, 1992 Count 14
- 8490 *Pangrapta decoralis* Hbn.
July 5, 1991 Count 1

8491	<i>Ledaea perditalis</i> (Wlk.) May 30, 1991–July 20, 1990.	Count 7
8499	<i>Metalectra discalis</i> (Grt.) June 27, 1991–Aug. 27, 1992.	Count 8
8500	<i>Metalectra quadrisignata</i> (Wlk.) July 27–Aug. 24, 1990.	Count 2
8514	<i>Scolecocampa liburnia</i> (Gey.) June 20, 1991–July 31, 1989.	Count 25
8555	<i>Scoliopteryx libatrix</i> (L.) July 8, 1988–Aug. 24, 1990.	Count 3
8587	<i>Panopoda rufimargo</i> (Hbn.) June 15, 1988–Aug. 7, 1992.	Count 97
8588	<i>Panopoda carneicosta</i> Gn. July 8, 1988–July 13, 1990.	Count 3
8689	<i>Zale lunata</i> (Drury) Sep. 21, 1990.	Count 1
8697	<i>Zale minerea</i> (Gn.) May 30, 1991–July 15, 1988.	Count 23
8704+	<i>Zale helata</i> (Sm.) June 8, 1990.	Count 1
8716	<i>Zale unilineata</i> (Grt.) June 15, 1988.	Count 1
8717	<i>Zale horrida</i> Hbn. June 12, 1989–July 19, 1991.	Count 5
8719	<i>Euparthenos nubilis</i> (Hbn.) June 26, 1989–July 24, 1992.	Count 4
8721	<i>Allotria elonympha</i> (Hbn.) June 1, 1988–July 4, 1989.	Count 8
8727	<i>Parallelia bistriaris</i> Hbn. June 1, 1988–Aug. 24, 1990.	Count 30
8738+	<i>Caenurgina crassiuscula</i> (Haw.) June 27, 1991–Sep. 10, 1988.	Count 17
8771	<i>Catocala piatrix</i> Grt. Sep. 9, 1989.	Count 1
8778	<i>Catocala habilis</i> Grt. Sep. 7, 1990–Sep. 13, 1991.	Count 2
8784	<i>Catocala obscura</i> Stkr. Sep. 2, 1989.	Count 1
8788	<i>Catocala relecta</i> Grt. Aug. 16–Sep. 21, 1990.	Count 12
8792	<i>Catocala vidua</i> (J.E. Smith) Sep. 7, 1990–Sep. 9, 1989.	Count 2
8795	<i>Catocala palaeogama</i> Gn. Aug. 27, 1992–Sep. 21, 1990.	Count 4
8796	<i>Catocala nebulosa</i> Edw. Sep. 2, 1989.	Count 1
8797	<i>Catocala subnata</i> Grt. July 12, 1991–Sep. 25, 1992.	Count 9
8798	<i>Catocala neogama</i> (J.E. Smith) July 31, 1989–Sep. 21, 1990.	Count 2
8801	<i>Catocala ilia</i> (Cram.) July 8, 1988–Aug. 27, 1992.	Count 16
8802	<i>Catocala cerogama</i> Gn. Aug. 24, 1990–Sep. 25, 1992.	Count 3
8832	<i>Catocala cara</i> Gn. Aug. 5, 1988–Sep. 9, 1989.	Count 4
8846	<i>Catocala sordida</i> Grt. Aug. 3, 1990.	Count 1
8851	<i>Catocala coccinata</i> Grt. July 8, 1988.	Count 1
8857	<i>Catocala ultronia</i> (Hbn.) July 5, 1991–Sep. 7, 1990.	Count 34
8858	<i>Catocala crataegi</i> Saund. July 20, 1990.	Count 1
8863	<i>Catocala nitra</i> Grt. July 5, 1991–Aug. 27, 1992.	Count 10
8864	<i>Catocala grynea</i> (Cram.) July 5, 1991–Sep. 9, 1989.	Count 64
8867	<i>Catocala blandula</i> Hulst July 8, 1988–Aug. 7, 1992.	Count 4
8878	<i>Catocala amica</i> (Hbn.) Aug. 16–Sep. 14, 1990.	Count 4
8878.1	<i>Catocala lineella</i> Grt. Aug. 27, 1992–Sep. 9, 1989.	Count 3
8881	<i>Abrostola urentis</i> Gn. June 27, 1991–Aug. 21, 1989.	Count 8
8887	<i>Trichopstia ni</i> (Hbn.) Sep. 10, 1988.	Count 1
8890	<i>Pseudophusia includens</i> (Wlk.) June 1, 1988.	Count 1
8898	<i>Allagrapha aerea</i> (Hbn.) June 6, 1991–Sep. 14, 1990.	Count 28
8904	<i>Chrysanypha formosa</i> (Grt.) July 13, 1990.	Count 1
8905	<i>Eosiphonopteryx thyatroides</i> (Gn.) July 20, 1990.	Count 1
8908	<i>Autographa precationis</i> (Gn.) May 18, 1988–Sep. 25, 1992.	Count 43
8924	<i>Anagrapha falcifera</i> (Kby.) June 1, 1988–Aug. 2, 1991.	Count 8
8955	<i>Marathyssa inficita</i> (Wlk.) June 22, 1988–Sep. 9, 1989.	Count 9
8956	<i>Marathyssa basalis</i> Wlk. May 28, 1989.	Count 2
8957	<i>Paectes oculatrix</i> (Gn.) June 6, 1991–Aug. 26, 1988.	Count 19
8970	<i>Baileya ophthaluica</i> (Gn.) May 18, 1988–June 26, 1989.	Count 56
8971	<i>Baileya doruntans</i> (Gn.) May 30–July 19, 1991.	Count 24
8972	<i>Baileya levitans</i> (Sm.) May 28–July 31, 1989.	Count 22
8973	<i>Baileya australis</i> (Grt.) June 1, 1988–July 12, 1991.	Count 2
8983	<i>Meganola minuscula</i> (Zell.) May 30, 1991–Aug. 14, 1989.	Count 37
8983.1	<i>Meganola phylla</i> (Dyar) May 30, 1991–Aug. 3, 1990.	Count 11
9037	<i>Hyperstrotia pervertens</i> (B. & McD.) June 13, 1991–July 27, 1990.	Count 80
9040	<i>Hyperstrotia secta</i> (Grt.) June 20, 1991–Aug. 5, 1988.	Count 4
9044	<i>Thioptera uigrofimbria</i> (Gn.) July 10, 1992.	Count 1
9047	<i>Lithacodia muscosa</i> (Gn.) June 6, 1991–Aug. 21, 1989.	Count 308

9048	<i>Lithacodia albidula</i> (Gn.) June 27–July 19, 1991	Count 5	9254	<i>Acronicta afflicta</i> Grt. May 30, 1991	Count 1
9051	<i>Lithacodia musta</i> (G. & R.) June 22, 1990–July 29, 1988	Count 2	9261	<i>Acronicta impressa</i> Wlk. July 27, 1990–Aug. 7, 1989	Count 2
9053	<i>Pseudeustrotia carneola</i> (Gn.) May 30–Sep. 13, 1991	Count 412	9272	<i>Acronicta obliuina</i> (J.E. Smith) June 1, 1990–July 31, 1989	Count 3
9055.1	<i>Maliattha synochitis</i> (G. & R.) May 30, 1991–July 22, 1988	Count 47	9285	<i>Polygrammate hebraicum</i> Hbn. May 30, 1991–July 27, 1990	Count 18
9056	<i>Homophoberia cristata</i> Morr. July 12, 1991	Count 1	9299	<i>Eudryas unio</i> (Hbn.) Aug. 16, 1990	Count 1
9057	<i>Homophoberia apicosa</i> (Haw.) June 8, 1990–Sep. 9, 1989	Count 41	9301	<i>Eudryas grata</i> (F.) May 30, 1991–Aug. 14, 1989	Count 34
9062	<i>Cerma cerintha</i> (Tr.) June 15, 1988–July 12, 1991	Count 16	9332	<i>Apamea vulgaris</i> (G. & R.) May 28, 1989	Count 1
9065	<i>Leuconycta diphteroides</i> (Gn.) May 30, 1991–Aug. 24, 1990	Count 36	9341	<i>Apamea vultuosa</i> (Grt.) June 6, 1991	Count 2
9066	<i>Leuconycta lepidula</i> (Grt.) May 30, 1991–Sep. 9, 1989	Count 9	9364	<i>Apamea sordens</i> (Hufn.) June 12, 1989–June 15, 1988	Count 2
9090	<i>Tarachidia caudifacta</i> (Hbn.) June 29, 1990–Aug. 26, 1988	Count 19	9367	<i>Apamea dubitans</i> (Wlk.) Aug. 31, 1990–Sep. 9, 1989	Count 2
9095	<i>Tarachidia erastrioides</i> (Gn.) May 30, 1991–Sep. 7, 1990	Count 48	9382	<i>Apamea devastator</i> (Brace) June 15, 1988	Count 2
9127	<i>Spragueia leo</i> (Gn.) July 27, 1990	Count 1	9404	<i>Oligia modica</i> (Gn.) Aug. 2, 1991–Aug. 31, 1990	Count 21
9184	<i>Colocasia flavicornis</i> (Sm.) July 12, 1991–Aug. 5, 1988	Count 28	9406	<i>Oligia fractilinea</i> (Grt.) July 19–Aug. 30, 1991	Count 15
9185	<i>Colocasia propinquilinea</i> (Grt.) May 28, 1989–Aug. 9, 1990	Count 186	9408	<i>Oligia exhausta</i> (Sm.) June 22, 1988–July 5, 1991	Count 2
9189	<i>Charadra deridens</i> (Gn.) June 1, 1988–Aug. 14, 1989	Count 5	9415	<i>Oligia bridghami</i> (G.&R.) July 19, 1991	Count 1
9193	<i>Raphia frater</i> Grt. May 30–Aug. 2, 1991	Count 15	9419	<i>Oligia mactata</i> (Gn.) July 3, 1992–Sep. 21, 1990	Count 2
9200	<i>Acronicta americana</i> (Harr.) May 30, 1991–July 17, 1989	Count 9	9427	<i>Meropleon diversicolor</i> (Morr.) Sep. 9, 1989	Count 1
9203	<i>Acronicta dactylina</i> Grt. June 15, 1988–Aug. 3, 1990	Count 3	9449	<i>Archana oblonga</i> (Grt.) July 19, 1991–Aug. 9, 1990	Count 3
9227	<i>Acronicta laetifica</i> Sm. June 15, 1988	Count 1	9454	<i>Amphipoea velata</i> (Wlk.) June 27, 1991–July 27, 1990	Count 25
9229	<i>Acronicta hasta</i> Gn. June 1, 1988–Aug. 27, 1992	Count 15	9457+	<i>Amphipoea americana</i> (Speyer) July 20, 1990–Sep. 4, 1992	Count 4
9235	<i>Acronicta spinigera</i> Gn. May 30, 1991–July 15, 1988	Count 26	9471	<i>Papaipema arctivorens</i> Hamp. Aug. 31–Sep. 21, 1990	Count 4
9236	<i>Acronicta morula</i> (G. & R.) June 1, 1988	Count 1	9473	<i>Papaipema impecuniosa</i> (Grt.) Sep. 25, 1992	Count 1
9237	<i>Acronicta interrupta</i> Gn. July 31, 1989–Aug. 16, 1990	Count 3	9483	<i>Papaipema inquaesita</i> (G. & R.) Aug. 19, 1988–Sep. 14, 1990	Count 6
9238	<i>Acronicta lobeliae</i> Gn. June 1–Aug. 16, 1990	Count 3	9485	<i>Papaipema baptisiae</i> (Bird) Sep. 10, 1988–Sep. 21, 1990	Count 6
9243	<i>Acronicta ovata</i> Grt. June 6, 1991–Aug. 5, 1988	Count 13	9505	<i>Papaipema cerussata</i> (Grt.) Sep. 10, 1988–Sep. 25, 1992	Count 7
9244	<i>Acronicta modia</i> Wlk. June 12, 1989–July 8, 1988	Count 4	9520	<i>Achatodes zeae</i> (Harr.) July 15, 1988–Aug. 21, 1992	Count 11
9245+	<i>Acronicta haesitata</i> (Grt.) May 30–Aug. 16, 1991	Count 374	9523	<i>Bellura gortynoides</i> (Wlk.) Aug. 3, 1990	Count 1
9246	<i>Acronicta clarescens</i> Gn. Sep. 2, 1989	Count 1	9525	<i>Bellura obliqua</i> (Wlk.) May 28, 1992–Aug. 14, 1989	Count 16
9251	<i>Acronicta retardata</i> (Wlk.) June 6–July 19, 1991	Count 7	9526	<i>Bellura densa</i> (Wlk.) June 15, 1988–Aug. 14, 1989	Count 7

9545	<i>Enplexia benesimilis</i> McD. May 30–Sep. 13, 1991.....	Count 82
9546	<i>Phlogophora iris</i> Gn. June 15, 1988.....	Count 1
9547	<i>Phlogophora periculosa</i> Gn. Aug. 14, 1989–Sep. 10, 1988.....	Count 30
9551	<i>Eiargia mephisto</i> Franc. July 3, 1992.....	Count 1
9555	<i>Ipinorpha pleonectusa</i> Grt. July 19, 1991–Aug. 31, 1990.....	Count 8
9556	<i>Chytonix palliatricula</i> (Gn.) May 30, 1991–July 31, 1989.....	Count 94
9578	<i>Hypna xylinoides</i> (Gn.) May 30, 1991–Aug. 31, 1990.....	Count 30
9582	<i>Nedra ramosula</i> (Gn.) Aug. 2, 1991.....	Count 1
9618	<i>Phosphila turbulenta</i> Hbn. July 5, 1991–July 15, 1988.....	Count 6
9619	<i>Phosphila miselioides</i> (Gn.) July 12, 1991.....	Count 1
9631	<i>Callopteria mollissima</i> (Gn.) June 1, 1990–Aug. 2, 1991.....	Count 12
9638	<i>Amphipyra pyramidoides</i> Gn. July 22, 1988–Sep. 25, 1992.....	Count 133
9647	<i>Athetis miranda</i> (Grt.) July 19, 1991–Aug. 14, 1989.....	Count 3
9650	<i>Anorthodes tarda</i> (Gn.) May 28–Sep. 25, 1992.....	Count 99
9662	<i>Balsa malana</i> (Fitch) July 27, 1990–Aug. 14, 1989.....	Count 2
9663	<i>Balsa tristigella</i> (Wlk.) May 30–July 12, 1991.....	Count 52
9664	<i>Balsa labecula</i> (Grt.) May 30, 1991–July 29, 1988.....	Count 25
9666	<i>Spodoptera frugiperda</i> (J.E. Smith) Aug. 26, 1988–Sep. 14, 1990.....	Count 3
9669	<i>Spodoptera ornithogalli</i> (Gn.) Aug. 26, 1988.....	Count 1
9678	<i>Elaphria versicolor</i> (Grt.) June 13, 1991–July 20, 1990.....	Count 12
9681	<i>Elaphria festivoidea</i> (Gn.) June 26–July 4, 1989.....	Count 3
9688	<i>Galgula partita</i> Gn. June 15–July 15, 1988.....	Count 5
9689	<i>Perigea xanthioides</i> Gn. May 30, 1991–Sep. 10, 1988.....	Count 49
9690	<i>Condica videns</i> (Gn.) July 24, 1989–Aug. 19, 1988.....	Count 2
9696	<i>Condica vecors</i> (Gn.) June 5, 1992–Aug. 21, 1989.....	Count 19
9720	<i>Ogdocoonta ciuereola</i> (Gn.) June 1, 1990–Sep. 9, 1989.....	Count 87
9815	<i>Cosmia calami</i> (Harv.) July 20, 1990–July 24, 1989.....	Count 7
9818	<i>Amolita fessa</i> Grt. June 20, 1991–July 17, 1992.....	Count 13
9952	<i>Eucirroedia pampina</i> (Gn.) Sep. 14, 1990.....	Count 1
9957	<i>Sutira bicolorago</i> (Gn.) Sep. 25, 1992.....	Count 1
9961	<i>Anathix ralla</i> (G. & R.) Aug. 14, 1989–Sep. 25, 1992.....	Count 141
10033	<i>Catabena lineolata</i> Wlk. May 21, 1989.....	Count 1
10059	<i>Homohadena badistriga</i> (Grt.) July 22, 1988.....	Count 1
10202	<i>Cucullia convexipennis</i> G. & R. Aug. 16, 1990.....	Count 1
10276	<i>Polia imbrifera</i> (Gn.) June 20, 1991–Aug. 14, 1989.....	Count 4
10288+	<i>Polia purpurisata</i> (Grt.) May 30, 1991–Aug. 9, 1990.....	Count 497
10292	<i>Melanchra adjuncta</i> (Gn.) May 28–Aug. 14, 1989.....	Count 8
10293	<i>Melanchra picta</i> (Harr.) June 22, 1988–Aug. 16, 1990.....	Count 3
10299	<i>Lacanobia subnigra</i> (G. & R.) June 8, 1988–Aug. 27, 1992.....	Count 6
10300	<i>Spiramater grandis</i> (Gn.) June 6, 1991.....	Count 1
10304	<i>Trichordestra legitima</i> (Grt.) June 15–July 8, 1988.....	Count 2
10348	<i>Lasiestra poca</i> (B. & Benj.) July 24, 1992.....	Count 4
10397	<i>Lacinipolia renigera</i> (Steph.) May 30–Sep. 13, 1991.....	Count 46
10405	<i>Lacinipolia lorea</i> (Gn.) May 30, 1991–July 10, 1992.....	Count 29
10436	<i>Aletia oxygala</i> (Grt.) May 30, 1991–Sep. 9, 1989.....	Count 14
10438	<i>Pseudaleia unipuncta</i> (Haw.) May 18–Sep. 10, 1988.....	Count 96
10444+	<i>Leucania phragmatidicola</i> Gn. June 1–Sep. 10, 1988.....	Count 9
10446+	<i>Leucania multilinea</i> Wlk. May 30–Aug. 30, 1991.....	Count 12
10447	<i>Leucania connuoides</i> Gn. July 19, 1991–Aug. 16, 1990.....	Count 4
10461+	<i>Leucania ursula</i> (Fbs.) June 6, 1991–Sep. 9, 1989.....	Count 72
10501	<i>Crocigrapha normani</i> (Grt.) May 18, 1988.....	Count 1
10521	<i>Morrisonia confusa</i> (Hbn.) May 18–June 15, 1988.....	Count 8
10521.1	<i>Morrisonia latex</i> (Gn.) June 1–July 22, 1988.....	Count 53
10524	<i>Nephelodes minians</i> Gn. Aug. 21, 1989–Sep. 25, 1992.....	Count 108
10532	<i>Homorthodes furfurata</i> (Grt.) June 27, 1991–July 27, 1990.....	Count 30
10563	<i>Protorthodes oviduca</i> (Gn.) June 12, 1992.....	Count 1
10578	<i>Pseudorthodes vecors</i> (Gn.) May 30, 1991–Sep. 4, 1992.....	Count 144
10585	<i>Orthodes crenulata</i> (Butler) June 22, 1988–Aug. 16, 1991.....	Count 19

10587	<i>Orthodes cynica</i> Gn. May 30, 1991–July 17, 1992.	Count 297
10627	<i>Tricholita signata</i> (Wlk.) Aug. 9, 1990–Sep. 10, 1988.	Count 14
10648	<i>Agrotis gladiaria</i> Morr. Sep. 14, 1990.	Count 1
10651	<i>Agrotis venerabilis</i> Wlk. Sep. 21, 1990–Sep. 25, 1992.	Count 7
10663	<i>Agrotis ipsilon</i> (Hufn.) May 28, 1992–Sep. 10, 1988.	Count 216
10674+	<i>Feltia subgothica</i> (Haw.) Aug. 2, 1991–Aug. 27, 1992.	Count 25
10676	<i>Feltia herilis</i> (Grt.) July 31, 1989–Sep. 14, 1990.	Count 73
10698.2	<i>Trichosilia geniculata</i> (G. & R.) Aug. 2, 1991–Sep. 10, 1988.	Count 5
10793	<i>Euxoa scholastica</i> McD. July 8–July 22, 1988.	Count 3
10870	<i>Richia acclivis</i> (Morr.) Aug. 21, 1989.	Count 1
10891	<i>Ochropleura plecta</i> (L.) May 30, 1991–Sep. 25, 1992.	Count 223
10903+	<i>Euagrotis illapsa</i> (Wlk.) July 19, 1991–Aug. 19, 1988.	Count 3
10911	<i>Anicla infecta</i> (Ochs.) July 19, 1991.	Count 1
10915	<i>Peridroma saucia</i> (Ochs.) July 5, 1991–Sep. 25, 1992.	Count 7
10917	<i>Diarsia rubifera</i> (Grt.) June 29, 1990.	Count 1
10926	<i>Spaelotis clandestina</i> (Harr.) June 22, 1990.	Count 1
10942.1+	<i>Xestia dolosa</i> Franc. May 28, 1989–Sep. 25, 1992.	Count 682
10943	<i>Xestia normaniana</i> (Grt.) Aug. 3–Sep. 21, 1990.	Count 157
10944	<i>Xestia smithii</i> (Snell.) Aug. 23, 1991–Sep. 14, 1990.	Count 23
10950+	<i>Xestia bicarnea</i> (Gn.) Aug. 2–Sep. 13, 1991.	Count 119
10954	<i>Xestia bugrai</i> Kocak Sep. 25, 1992.	Count 1
10998	<i>Choephora fungorum</i> G. & R. Sep. 7–Sep. 21, 1990.	Count 6
11006	<i>Protolampra brunneicollis</i> (Grt.) June 22, 1990–Sep. 9, 1989.	Count 13
11007+	<i>Eueretagrotis sigmoides</i> (Gn.) July 8–July 22, 1988.	Count 5
11010	<i>Heptagrotis phyllophora</i> (Grt.) June 26–Sep. 9, 1989.	Count 4
11012	<i>Cryptocala acadensis</i> (Bethune) July 20, 1990.	Count 1
11029+	<i>Abagrotis alternata</i> (Grt.) June 13, 1991–Sep. 25, 1992.	Count 69

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CHECKLIST OF THE MOTHS OF GRAND RIVER TERRACES PRESERVE, ASHTABULA COUNTY, OHIO (1988-1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Grand River Terraces Preserve in Ashtabula County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988-1992) and includes 30,087 specimens representing 520 species. The study began in 1987 and continued through 1996, but only data for 1988-1992 are included here. The checklist is a historical record of the species that were present in 1988-1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after ten years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988-1992 is 6.53 and the Shannon-Wiener Evenness Index is 0.72. Two hundred nineteen of the 520 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. Eighty-three of the 219 widespread species had counts of less than 10 at Grand River Terraces. Three species of owl moths that were collected at Grand River Terraces are of special interest in Ohio. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Introduction

The objective of this study was to document the population changes of native moths for ten years at several sites within the drainage basin of the Grand River in Trumbull, Ashtabula, and Lake Counties, Ohio, during gypsy moth invasion and control. This is the fourth in a series of six checklists that tabulate the moths collected at each site during 1988–1992.

Over this same period, the population of the gypsy moth increased in the entire drainage basin. Pheromone trap catches of male gypsy moths increased at Grand River Terraces Preserve from $7 \pm 2(4)$ per trap in 1987 [mean \pm standard error (number of traps)], to $29 \pm 7(4)$ in 1988, $85 \pm 32(4)$ in 1989, $191 \pm 67(4)$ in 1990, and $344 \pm 60(4)$ in 1991. Pheromone trapping was discontinued after 1991. Ultraviolet-light-trap catches of male gypsy moths also increased, from 2 in 1987, to 7 in 1988, 52 in 1989, 109 in 1990, 54 in 1991, and 185 in 1992, but noticeable defoliation was not observed at Grand River Terraces Preserve.

The overall study provides baseline data on pre-outbreak moth diversity, as well as data on the impact of gypsy moth control agents.

Description of the Surveillance Site at Grand River Terraces Preserve

Grand River Terraces, a preserve of The Cleveland Museum of Natural History, is composed of 218 ha of mixed mesophytic forest and hemlock swamp forest (Bissell, 1998) and includes 1.6 km of frontage on the Grand River. The

Preserve spans Schweitzer (misspelled as Sweitzer on the topographic map) Road, Tote Road, and the Grand River (Anonymous, 1995). The Preserve is situated on swampy glacial lake plain with fine-grained lacustrine silt and clay soils (White and Totten, 1979, p. 7, Pl. 1) overlain by rich organic muck.

The light trap at Grand River Terraces Preserve was located in Morgan Township in Ashtabula County at latitude $41^{\circ} 42' 19''$ N and longitude $80^{\circ} 52' 53''$ W (U.S. Geological Survey East Trumbull and Jefferson, Ohio, 7.5-minute quadrangle topographic maps; Figure 1).

Grand River Terraces Preserve is located approximately 30 km northeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

The composition of the canopy and understory was evaluated for the 2500 m² of forest centered on the surveillance trap (point-quarter technique, nine points; Cottam and Curtis, 1956; Cox, 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90 m at Grand River Terraces. The importance values for the woody plants at the surveillance site at Grand River Terraces Preserve are given in Table 1.

The herbaceous plants included: State-threatened dewdrop *Dalibarda repens* L.; State-endangered moun-

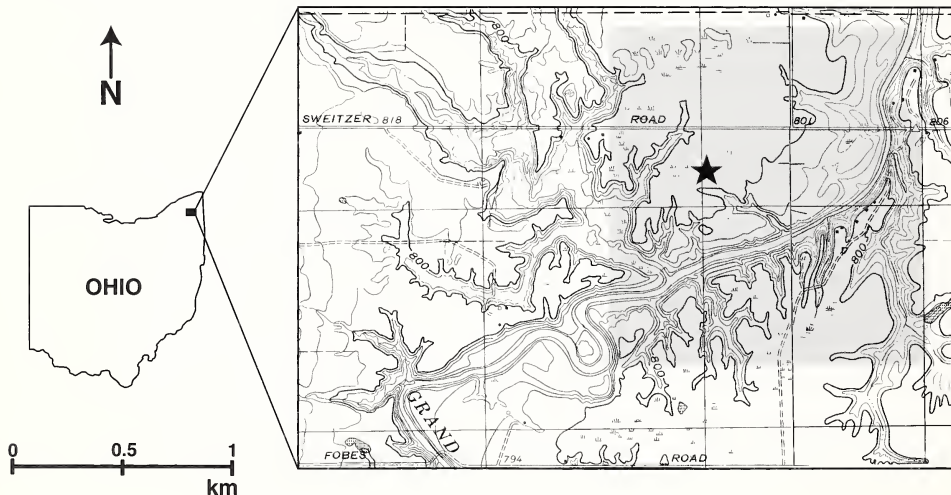


Figure 1. Map of the study area (adapted from the U.S. Geological Survey East Trumbull and Jefferson, Ohio 7.5-minute quadrangle topographic maps). Shaded area delineates Grand River Terraces Preserve; star indicates position of surveillance trap within the Preserve.

Table 1. Importance values for woody plants at the surveillance site at Grand River Terraces Preserve. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Woody Plant Species		Canopy	Understory
Maple, red	<i>Acer rubrum</i> L.	77	0
Beech, American	<i>Fagus grandifolia</i> Ehrh.	73	101
Maple, sugar	<i>Acer saccharum</i> Marsh.	69	168
Cherry, black	<i>Prunus serotina</i> Ehrh.	40	0
Tuliptree	<i>Liriodendron tulipifera</i> L.	24	0
Ash	<i>Fraxinus</i> spp.	17	0
Grape, summer	<i>Vitis aestivalis</i> Michx.	0	18
Hop Hornbeam, eastern	<i>Ostrya virginiana</i> (Mill.) K. Koch	0	14

tain rice-grass *Oryzopsis asperifolia* Michx.; State-threatened brownish sedge *Carex brunnescens* (Pers.) Poir., which is found nowhere else in Ohio; and toothwort *Cardamine maxima* (Nutt.) Wood, which is also found nowhere else in Ohio (Bissell, 1998; author citations according to Kartesz, 1994). These species were selected from a longer list of Grand River Terraces species on deposit in the Herbarium at The Cleveland Museum of Natural History.

An inventory of all plant species in the immediate vicinity of the trap was done in 1993 (James K. Bissell, 1998, personal communication). The spindle tree *Euonymus obovatus* Nutt. is one of the plants noted (author citation according to Kartesz, 1994). The third most abundant moth species feeds on euonymus.

Surveillance Techniques

One Ellisco®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, from late May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were computerized. All the specimens collected are deposited in the Insect Collection at The Cleveland Museum of Natural History.

Results and Discussion

A total of 30,087 specimens representing 520 species were collected in 1988–1992 (Appendix). Species were identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al.

(1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodges et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 32 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1987 to 1996, is shown in Figure 2. In 1987 (not included in this checklist), 316 species were collected, and in 1996, after ten years, the total had reached 592 (1993–1996, also not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Grand River Terraces Preserve and five years would have been a minimum. The species accumulation curve was still rising after ten years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: fall, winter, and early spring moths are missing because collecting was not begun until the end of May and collecting ended in September. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

Relative abundances of the 520 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The Shannon-Wiener Diversity Index is 6.53 and the Shannon-Wiener Evenness Index is 0.72.

Over 20 percent of the total count was composed of lesser maple spanworm moth *Itame pustularia* (6273), and red and sugar maples (together with American beech) are dominants in the canopy and understory. The next most abundant species was banded tussock moth

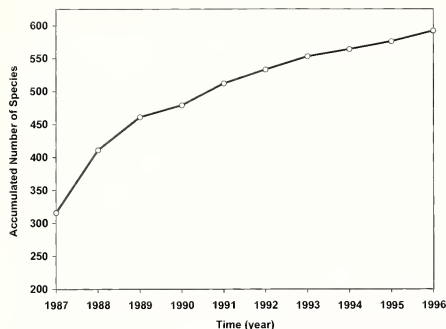


Figure 2. Plot of the annual accumulation of species collected at Grand River Terraces Preserve, 1987–1996.

Halysidota tessellaris (8203+) whose larva feeds on many deciduous trees. Following, in order of decreasing abundance, were: American ermine moth *Yponomeuta multipunctella* (2420) whose larva feeds on euonymous; disparaged arches *Polia detracta* (10288+) whose larva feeds on clover, blueberries, oaks, etc.; esther moth *Hypagyrtis esther* (6655) whose larva feeds on pines; cynical quaker *Orthodes cynica* (10587) whose larva feeds on plantain, dandelion, and developing goldenrod blossoms; forest tent caterpillar moth *Malacosoma disstria* (7698) whose

larva feeds on trees and shrubs, especially aspens and maples; sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants; gypsy moth *Lymantria dispar* (8318) whose larva feeds on shrubs and trees, especially oak; and pale beauty *Campaea perlata* (6796) whose larva feeds on a variety of deciduous trees.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 219 Grand River Terraces species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988; 1990). Three explanations have been proposed (Krebs, 1994). First, the relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not exist, when abundance is viewed from the perspective of abundance at Grand River Terraces. Of the 219 Grand River Terraces species which are widespread in northeast Ohio, 83 had total counts of 10 or fewer at Grand River Terraces.

Overall, there is a close correspondence between the number of widespread species in an abundance interval

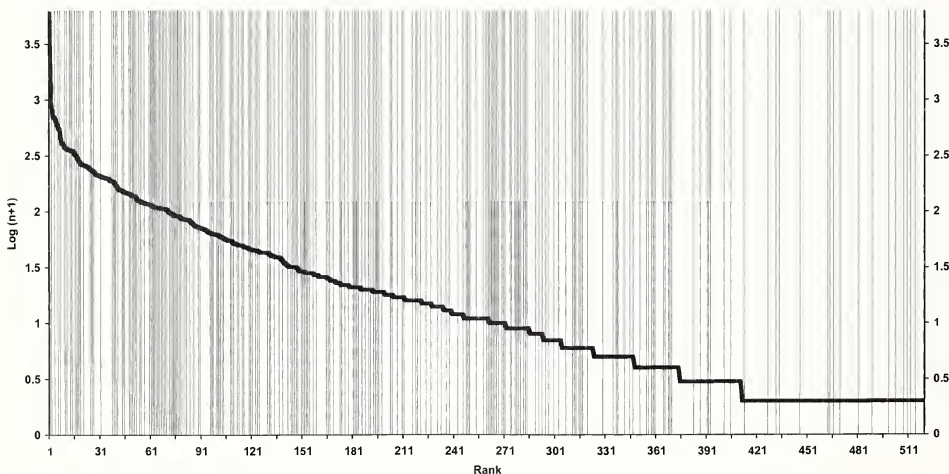


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Grand River Terraces Preserve, 1988–1992.

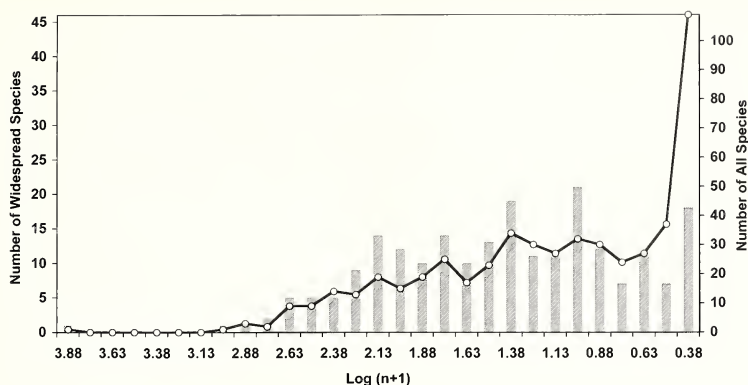


Figure 4. Correspondence between the total number of Grand River Terraces species in an abundance interval (line, scale at right) and the number of widespread Grand River Terraces species in the same abundance interval (bar, scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

and the total number of species (Figure 4). Only the decrease in the proportion of widespread species in the singleton and doubleton intervals conforms to expectation.

Three species of owlet moths collected at Grand River Terraces are listed as being of special interest in Rings et al. (1992): *Enargia decolor* (9549) whose larva feeds on trembling aspen, speckled alder, and willow; *Enargia infumata* (9550) whose larva feeds on trembling aspen and willow; and scurfy quaker *Homorthodes fufurata* (10532) whose larva feeds on maples.

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Appendix. Checklist of species collected at Grand River Terraces, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection, and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family OECOPHORIDAE

882	<i>Agonopterix robinella</i> (Pack.) June 22–July 29, 1988	Count 20
951	<i>Machimia tentoriferella</i> Clem. Sep. 10, 1992	Count 1
957	<i>Psilocorsis reflexella</i> Clem. June 1, 1988–Aug. 21, 1989	Count 42
1014+	<i>Antaeotricha lencillana</i> (Zell.) May 18, 1988–Aug. 30, 1991	Count 349
1046	<i>Callima argenticinctella</i> Clem. June 27, 1991–Aug. 16, 1990	Count 7

Family YPONOMEUTIDAE

2401	<i>Atteva punctella</i> (Cram.) July 29, 1988	Count 1
2420	<i>Yponomeuta multipunctella</i> Clem. June 20, 1991–Aug. 7, 1992	Count 712

Family TORTRICIDAE

2863	<i>Hedya chionosema</i> (Zell.) July 29, 1988	Count 1
3186	<i>Epiblema scudderiana</i> (Clem.) June 1, 1988	Count 1
3361	<i>Ancylis semiovana</i> (Zell.) Aug. 5, 1988	Count 3
3504	<i>Croesia curvatana</i> (Kft.) June 26, 1989–July 8, 1988	Count 3
3540	<i>Acleris logiana</i> (Cl.) May 18, 1988	Count 13
3594	<i>Pandemis limitata</i> (Rob.) June 12, 1989–Sep. 10, 1988	Count 90
3623	<i>Argyrotaenia quercifolia</i> (Fitch) June 6, 1991–July 4, 1989	Count 25
3624	<i>Argyrotaenia alisellana</i> (Rob.) June 26, 1992	Count 1
3625	<i>Argyrotaenia mariana</i> (Fern.) May 21–June 4, 1989	Count 11
3632	<i>Choristoneura fractivittana</i> (Clem.) May 30, 1991–Aug. 26, 1988	Count 359
3633	<i>Choristoneura parallela</i> (Rob.) June 22, 1988–Sep. 10, 1992	Count 54
3635	<i>Choristoneura rosaceana</i> (Harr.) June 15–Aug. 24, 1990	Count 102
3648	<i>Archips argyrospila</i> (Wlk.) June 1–July 8, 1988	Count 116
3658	<i>Archips purpurana</i> (Clem.) July 8, 1988–July 10, 1989	Count 2
3661	<i>Archips cerasivorana</i> (Fitch) June 1, 1988	Count 5
3672	<i>Syndemis afflictana</i> (Wlk.) May 18–July 8, 1988	Count 22
3686	<i>Clepsis melaleucana</i> (Wlk.) June 1, 1988–June 26, 1989	Count 69
3720	<i>Sparganothis reticulatana</i> (Clem.) July 15, 1988–Aug. 27, 1992	Count 28

3725	<i>Sparganothis pettitana</i> (Rob.) June 22, 1988–July 20, 1990	Count 15
3748	<i>Amorbia humerosana</i> Clem. June 1, 1988–June 26, 1989	Count 2

Family LIMACODIDAE

4652	<i>Tortricidia testacea</i> Pack. May 30–July 19, 1991	Count 106
4654	<i>Tortricidia flexuosa</i> (Grt.) June 6–Aug. 23, 1991	Count 250
4659	<i>Packardia geminata</i> (Pack.) June 12, 1989–June 27, 1991	Count 9
4661	<i>Packardia elegans</i> (Pack.) June 6, 1991–July 24, 1992	Count 15
4665	<i>Lithacodes fasciola</i> (H.-S.) June 6, 1991–Aug. 7, 1989	Count 42
4667	<i>Apoda y-inversum</i> (Pack.) June 22, 1988–July 24, 1992	Count 23
4669	<i>Apoda biguttata</i> (Pack.) June 15, 1988	Count 1
4681	<i>Isa textula</i> (H.-S.) June 26, 1989–July 15, 1988	Count 6
4685	<i>Adoneta spinuloides</i> (H.-S.) June 20, 1991–Aug. 7, 1992	Count 4
4697	<i>Enoclea delphinii</i> (Bdv.) June 15, 1988–July 20, 1990	Count 6

Family CRAMBIDAE

4703	<i>Gesneria centuriella</i> (D. & S.) June 1, 1988–Sep. 9, 1989	Count 211
4748	<i>Mimroessa icciusalis</i> (Wlk.) June 15, 1988–Aug. 14, 1989	Count 8
4751	<i>Mimroessa gyralis</i> (Hulst) July 8, 1988–Aug. 7, 1992	Count 2
4889	<i>Dicymolomia julianalis</i> (Wlk.) June 8, 1988–Sep. 9, 1989	Count 3
4897	<i>Evergestis pallidata</i> (Hufn.) June 6–Sep. 13, 1991	Count 26
4936	<i>Saucrobotys finitialis</i> (Led.) June 12, 1992–Aug. 2, 1991	Count 4
4937	<i>Nascia acutella</i> (Wlk.) Aug. 19, 1988	Count 1
4944	<i>Crocidophora serratissimalis</i> Zell. June 1, 1990–Aug. 30, 1991	Count 31
4945	<i>Crocidophora tuberculalis</i> Led. June 15, 1988–Sep. 7, 1992	Count 85
4949	<i>Ostrinia mbilalis</i> (Hbn.) June 5, 1992–Aug. 23, 1991	Count 24
4950	<i>Fumibotys finitialis</i> (Gn.) Aug. 7, 1992–Aug. 21, 1989	Count 4
4951	<i>Perispasta caeculalis</i> Zell. Aug. 5, 1988	Count 1
4953a	<i>Phlyctaenia coronata tertialis</i> (Gn.) July 12–Aug. 2, 1991	Count 4

4962	<i>Hahncappisia marculenta</i> (G. & R.) June 1–Sep. 10, 1988.....	Count 8
5040	<i>Pyrausta bicoloralis</i> (Gn.) June 6, 1991–Sep. 21, 1990.....	Count 17
5071	<i>Pyrausta acronalis</i> (Wlk.) Aug. 16, 1990.....	Count 1
5079	<i>Udea rubigalis</i> (Gn.) June 6, 1991–Sep. 9, 1989.....	Count 65
5142	<i>Diacme clealis</i> (Wlk.) July 4–Aug. 14, 1989.....	Count 44
5156	<i>Nomophila nearctica</i> Mun. June 15, 1988–Aug. 2, 1991.....	Count 4
5159	<i>Desmia funeralis</i> (Hbn.) May 30, 1991–Sep. 9, 1989.....	Count 112
5182	<i>Blepharomastix ranalis</i> (Gn.) June 20, 1991–July 20, 1990.....	Count 4
5226	<i>Palpita magniferalis</i> (Wlk.) June 1, 1990–Sep. 6, 1991.....	Count 154
5228	<i>Polygrammodes flavidalis</i> (Gn.) June 20, 1991–Aug. 27, 1992.....	Count 8
5241	<i>Pantographa limata</i> (G. & R.) June 20, 1991–Aug. 24, 1990.....	Count 275
5272	<i>Herpetogramma bipunctalis</i> (F.) June 15, 1988–Sep. 9, 1989.....	Count 12
5275	<i>Herpetogramma pertextalis</i> (Led.) July 4–Aug. 21, 1989.....	Count 68
5277	<i>Herpetogramma thestealis</i> (Wlk.) Aug. 21, 1989.....	Count 1
5280	<i>Herpetogramma aeglealis</i> (Wlk.) July 17–Aug. 27, 1992.....	Count 70
5362+	<i>Crambus agitatellus</i> Clem. June 15–Sep. 10, 1988.....	Count 412
5464	<i>Urola nivalis</i> (Drury) July 5, 1991–July 27, 1990.....	Count 4
5465	<i>Vaxi auratella</i> (Clem.) July 15, 1988–Aug. 3, 1990.....	Count 2

Family PYRALIDAE

5518	<i>Aglossa cuprina</i> Zell. June 15, 1988–Aug. 31, 1990.....	Count 188
5524	<i>Hypsopygia costalis</i> (F.) June 15–July 15, 1988.....	Count 9
5532	<i>Herculia infimbrialis</i> Dyar July 15, 1988–July 31, 1989.....	Count 6
5533	<i>Herculia olinalis</i> (Gn.) July 4, 1989–Aug. 9, 1990.....	Count 6
5552	<i>Galasa nigrinodis</i> (Zell.) July 5–July 12, 1991.....	Count 2
5556	<i>Tosale oviplagalis</i> (Wlk.) July 4, 1989–Sep. 29, 1988.....	Count 13
5571	<i>Condylotomia participalis</i> Grt. June 29–Aug. 16, 1990.....	Count 158
5577	<i>Epipaschia superatalis</i> Clem. June 27, 1991–Aug. 5, 1988.....	Count 5
5606	<i>Tetralopha asperatella</i> (Clem.) July 13, 1990.....	Count 1
5997	<i>Euzophera ostricolorella</i> Hulst June 15, 1988–Sep. 7, 1990.....	Count 10
6053	<i>Peoria approximella</i> (Wlk.) July 12, 1991–July 20, 1990.....	Count 2

Family THYRIDIDAE

6079	<i>Dysodia granulata</i> (Neum.) Aug. 5, 1988.....	Count 2
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Family THYATRIDAE

6235	<i>Habrosyne scripta</i> (Gosse) May 30, 1991–June 8, 1990.....	Count 2
6237	<i>Pseudothyatira cynatophoroides</i> (Gn.) May 30, 1991–Aug. 5, 1988.....	Count 5

Family DREPANIDAE

6251	<i>Drepana arcuata</i> Wlk. May 30, 1991–Aug. 24, 1990.....	Count 5
6253	<i>Eudeilinia herminiata</i> (Gn.) June 6, 1991.....	Count 1
6255	<i>Oreta rosea</i> (Wlk.) June 6, 1991–Sep. 2, 1989.....	Count 19

Family GEOMETRIDAE

6261	<i>Helimata cycladata</i> G. & R. May 30, 1991.....	Count 2
6270	<i>Protitame virginialis</i> (Hulst) May 30, 1991–Aug. 5, 1988.....	Count 15
6273	<i>Eumacaria pustularia</i> (Wlk.) June 6–Sep. 13, 1991.....	Count 6302
6299	<i>Itame coartaria</i> (Hulst) June 20, 1991–July 10, 1989.....	Count 5
6303	<i>Itame subcessaria</i> (Wlk.) June 20, 1991–July 24, 1992.....	Count 17
6335+	<i>Semiothisa aequiferaria</i> (Wlk.) May 30, 1991–Sep. 14, 1990.....	Count 114
6342	<i>Semiothisa bisignata</i> (Wlk.) June 15–July 15, 1988.....	Count 5
6344+	<i>Semiothisa signaria</i> (Hbn.) May 18, 1988–Sep. 9, 1989.....	Count 87
6353	<i>Semiothisa multilineata</i> (Pack.) Aug. 7, 1989.....	Count 1
6386	<i>Semiothisa ocellinata</i> (Gn.) Aug. 2, 1991.....	Count 1
6583	<i>Anacamptodes ephyriaria</i> (Wlk.) June 27–July 12, 1991.....	Count 20
6584	<i>Anacamptodes humaria</i> (Gn.) Aug. 23, 1991.....	Count 1
6588	<i>Iridopsis larvata</i> (Gn.) May 18, 1988–Sep. 7, 1990.....	Count 96
6590	<i>Anavitrinella pampinaria</i> (Gn.) June 1, 1988–Aug. 21, 1989.....	Count 28
6597	<i>Ectropis crepuscularia</i> (D. & S.) June 6, 1991–Sep. 25, 1992.....	Count 241
6598	<i>Protoboarmia porcellaria</i> (Gn.) June 15, 1988–Sep. 25, 1992.....	Count 15
6599	<i>Epimecis hortaria</i> (F.) May 18, 1988–Aug. 24, 1990.....	Count 71
6620+	<i>Melanolophia canadaria</i> (Gn.) May 18, 1988–Aug. 27, 1992.....	Count 324
6638	<i>Eufidonia notataria</i> (Wlk.) June 12, 1992.....	Count 1
6640a	<i>Biston betularia cognataria</i> (Gn.) May 30, 1991–Aug. 9, 1990.....	Count 10
6654	<i>Hypagyrtis unipunctata</i> (Haw.) June 5, 1992–Sep. 21, 1990.....	Count 49

6655	<i>Hypagyrtis esther</i> (Barnes) May 30, 1991–Sep. 9, 1989.....	Count 631	6840	<i>Plagodis serinaria</i> H.-S. May 18, 1988–June 26, 1989.....	Count 235
6656	<i>Hypagyrtis pinitata</i> (Pack.) June 26, 1992.....	Count 1	6841	<i>Plagodis knetzingi</i> (Grt.) June 1, 1988–June 19, 1989.....	Count 8
6667	<i>Lomographa vestaliata</i> (Gn.) May 28, 1992–Aug. 9, 1990.....	Count 91	6842	<i>Plagodis phlogosaria</i> (Gn.) May 21–July 31, 1989.....	Count 13
6668	<i>Lomographa glomeraria</i> (Grt.) May 21, 1989–June 5, 1992.....	Count 3	6844	<i>Plagodis alcoalaria</i> (Gn.) May 18, 1988–Aug. 21, 1989.....	Count 61
6677	<i>Cabera erythemaria</i> Gn. May 18, 1988–Sep. 9, 1989.....	Count 264	6863	<i>Caripeta divisata</i> Wlk. June 20, 1991–Aug. 27, 1992.....	Count 14
6678	<i>Cabera variolaria</i> Gn. June 1–June 22, 1988.....	Count 2	6884	<i>Besma endropiaria</i> (G. & R.) May 30, 1991–Aug. 24, 1990.....	Count 220
6680	<i>Cabera quadrifasciaria</i> (Pack.) June 15, 1988.....	Count 1	6885	<i>Besma quercivoraria</i> (Gn.) May 21–Sep. 9, 1989.....	Count 21
6720	<i>Lytrois militaria</i> (H.-S.) June 6, 1991–July 17, 1989.....	Count 148	6892	<i>Lambdina pellicidaria</i> (G. & R.) May 30, 1991.....	Count 1
6724	<i>Enchlaena serrata</i> (Drury) June 15, 1990–July 15, 1988.....	Count 3	6906	<i>Nepytia canosaria</i> (Wlk.) Sep. 21, 1990–Sep. 25, 1992.....	Count 3
6725	<i>Enchlaena imzaria</i> (Wlk.) May 30, 1991–July 3, 1992.....	Count 25	6912	<i>Sicya macularia</i> (Harr.) June 13, 1991–July 10, 1989.....	Count 42
6729	<i>Enchlaena johnsonaria</i> (Fitch) Aug. 2, 1991–Aug. 26, 1988.....	Count 5	6941	<i>Ensarca confusaria</i> Hbn. June 27, 1991–Sep. 10, 1988.....	Count 12
6739	<i>Enchlaena irraria</i> (B. & McD.) May 30, 1991–June 22, 1988.....	Count 7	6963	<i>Tetracis crocallata</i> Gn. May 30, 1991–July 8, 1988.....	Count 10
6740+	<i>Xanthotype urticaria</i> Swett May 30, 1991–Aug. 24, 1990.....	Count 24	6964	<i>Tetracis cachexiata</i> Gn. May 28–July 3, 1992.....	Count 187
6753+	<i>Pero honestaria</i> (Wlk.) May 21, 1989–Aug. 24, 1990.....	Count 107	6965	<i>Engonabapta nivosaria</i> (Gn.) June 13, 1991–Aug. 21, 1989.....	Count 347
6763	<i>Nacophora quernaria</i> (J.E. Smith) June 15–June 29, 1988.....	Count 5	6966	<i>Eutrapela clemataria</i> (J.E. Smith) May 18, 1988–Sep. 9, 1989.....	Count 185
6796	<i>Campaea perlata</i> (Gn.) May 30, 1991–Sep. 14, 1990.....	Count 372	6982	<i>Prochoerodes transversata</i> (Drury) June 20, 1991–Sep. 21, 1990.....	Count 77
6797	<i>Ennomos magnaria</i> Gn. July 19, 1991–Sep. 24, 1988.....	Count 5	6987	<i>Antepione thisoaria</i> (Gn.) July 5, 1991–Aug. 7, 1989.....	Count 2
6798	<i>Ennomos subsignaria</i> (Hbn.) June 13, 1991–Aug. 21, 1992.....	Count 203	7009	<i>Nematocampa limbata</i> (Haw.) June 20, 1991–Sep. 9, 1989.....	Count 202
6813	<i>Homochlodes disconventa</i> (Wlk.) June 15, 1990–June 19, 1989.....	Count 3	7046+	<i>Nemoria bistriaria</i> Hbn. July 5, 1991–Aug. 27, 1992.....	Count 31
6819	<i>Metanema inatoma</i> Gn. June 1–July 8, 1988.....	Count 11	7047	<i>Nemoria rubrifrontaria</i> (Pack.) June 1, 1988.....	Count 1
6822	<i>Metarranthis duaria</i> (Gn.) June 4, 1989–June 12, 1992.....	Count 2	7048	<i>Nemoria minosaria</i> (Gn.) June 4, 1989–Aug. 16, 1990.....	Count 4
6823	<i>Metarranthis angularia</i> B. & McD. May 30, 1991–June 26, 1989.....	Count 5	7053	<i>Dichorda iridaria</i> (Gn.) July 19, 1991.....	Count 1
6825	<i>Metarranthis indeclinata</i> (Wlk.) June 5–June 19, 1992.....	Count 16	7058	<i>Synchlora acerata</i> (F.) May 30–Aug. 30, 1991.....	Count 6
6826	<i>Metarranthis hypocharia</i> (H.-S.) June 1, 1988–July 3, 1992.....	Count 106	7132	<i>Pleuropracha insularia</i> (Gn.) June 20–Sep. 6, 1991.....	Count 55
6827	<i>Metarranthis refractaria</i> (Gn.) July 3, 1992.....	Count 1	7136	<i>Cyclophora packardii</i> (Prout) May 30, 1991–Sep. 9, 1989.....	Count 8
6828	<i>Metarranthis homuraria</i> (G. & R.) June 15, 1988.....	Count 2	7139	<i>Cyclophora pendulinaria</i> (Gn.) Aug. 5, 1988.....	Count 1
6834	<i>Cepphis decoloraria</i> (Hulst) July 3, 1992.....	Count 1	7146	<i>Haematopsis grataria</i> (F.) Sep. 9, 1989.....	Count 2
6835	<i>Cepphis armataria</i> (H.-S.) June 20, 1991–July 15, 1988.....	Count 6	7157	<i>Scopula cacaminaria</i> (Morr.) June 15–June 22, 1990.....	Count 2
6836	<i>Anagoga occidnaria</i> (Wlk.) May 18–Aug. 19, 1988.....	Count 26	7159	<i>Scopula limboundata</i> (Haw.) June 15, 1990–Sep. 10, 1988.....	Count 174
6838+	<i>Probole amicaria</i> (H.-S.) May 28, 1992–Aug. 14, 1989.....	Count 229	7169	<i>Scopula inductata</i> (Gn.) June 26–Aug. 14, 1989.....	Count 2

- 7189 *Dysstroma hersiliata* (Gn.)
May 30, 1991–July 17, 1989..... Count 25
- 7196+ *Eulithis diversilineata* (Hbn.)
June 20, 1991–Sep. 25, 1992..... Count 167
- 7236+ *Hydriomena renunciata* (Wlk.)
May 21, 1989–June 8, 1990..... Count 2
- 7292 *Hydria prunivora* (Fgn.)
June 1, 1988–July 20, 1990..... Count 5
- 7307 *Mesolenca ruficollata* (Gn.)
June 15, 1988–July 24, 1989..... Count 3
- 7329 *Anticlea vasiliata* Gn.
May 21, 1989..... Count 1
- 7330 *Anticlea multifurcata* (Wlk.)
June 15, 1988..... Count 1
- 7333 *Stannodes gibbicostata* (Wlk.)
Sep. 6, 1991–Sep. 25, 1992..... Count 4
- 7368 *Xanthorhoe labradorensis* (Pack.)
July 19, 1991–Sep. 25, 1992..... Count 120
- 7388 *Xanthorhoe ferrugata* (Cl.)
May 30, 1991–Sep. 7, 1990..... Count 7
- 7390 *Xanthorhoe lacustrata* (Gn.)
May 21, 1989–Sep. 10, 1988..... Count 46
- 7394 *Epirrhoe alternata* (Muller)
May 30, 1991–Aug. 27, 1992..... Count 16
- 7399a *Euphyia unangulata intermedia* (Gn.)
May 30, 1991–Sep. 9, 1989..... Count 27
- 7414 *Orithonama obstipata* (F.)
May 30, 1991–Sep. 14, 1990..... Count 42
- 7416 *Orithonama centrostrigaria* (Woll.)
May 30, 1991–Sep. 25, 1992..... Count 109
- 7422 *Hydrelia inornata* (Hulst)
May 30–Aug. 16, 1991..... Count 25
- 7423 *Hydrelia albifera* (Wlk.)
May 30, 1991–Aug. 21, 1989..... Count 12
- 7430 *Trichodezia albovittata* (Gn.)
June 12, 1989–Aug. 5, 1988..... Count 2
- 7440 *Eubaphe mendica* (Wlk.)
June 6–July 19, 1991..... Count 124
- 7445 *Horisme intestinata* (Gn.)
May 30, 1991–Sep. 9, 1989..... Count 49
- 7474+ *Eupithecia miserulata* Grt.
May 18, 1988–Sep. 25, 1992..... Count 200
- 7640 *Lobophora nivergerata* Wlk.
May 21–June 19, 1989..... Count 11
- 7647 *Heterophleps triguttaria* H.-S.
May 30–Sep. 13, 1991..... Count 30
- 7648 *Dyspteris abortivaria* (H.-S.)
May 30–Aug. 2, 1991..... Count 21

Family EPIPLEMIDAE

- 7653 *Calledapteryx dryopterata* Grt.
Aug. 16, 1990..... Count 1

Family MIMALLONIDAE

- 7662 *Cicinnus melsheimeri* (Harr.)
July 3, 1992..... Count 1

Family APATELODIDAE

- 7663 *Apateles torrefacta* (J.E. Smith)
June 20, 1991–July 15, 1988..... Count 8

- 7665 *Olceclostera angelica* (Grt.)
June 12, 1992–July 15, 1988..... Count 8

Family LASIOCAMPIDAE

- 7670 *Tolype velleda* (Stoll)
May 21, 1989–Sep. 24, 1988..... Count 59
- 7673 *Tolype laricis* (Fitch)
July 12, 1991–Sep. 9, 1989..... Count 34
- 7687 *Phyllodesma americana* (Harr.)
May 28, 1989..... Count 1
- 7698 *Malacosoma dissidia* Hbn.
June 20, 1991–July 24, 1992..... Count 539
- 7701 *Malacosoma americanum* (F.)
June 6, 1991–July 13, 1990..... Count 84

Family SATURNIIDAE

- 7715 *Dryocampa rubicunda* (F.)
May 30, 1991–July 29, 1988..... Count 51
- 7746 *Automeris io* (F.)
May 30, 1991–July 13, 1990..... Count 27
- 7757 *Antheraea polyphemus* (Cram.)
May 30, 1991–July 15, 1988..... Count 15
- 7758 *Actias luna* (L.)
May 30, 1991–Aug. 27, 1992..... Count 18
- 7765 *Callosamia angulifera* (Wlk.)
July 15, 1988–July 31, 1989..... Count 4

Family SPHINGIDAE

- 7787 *Ceratomia undulosa* (Wlk.)
June 6, 1991–July 20, 1990..... Count 7
- 7821 *Smerinthus jamaicensis* (Drury)
July 19, 1991–Aug. 16, 1990..... Count 2
- 7824 *Paonias excaecatus* (J.E. Smith)
May 30, 1991–July 31, 1992..... Count 105
- 7825 *Paonias myops* (J.E. Smith)
May 30, 1991–July 29, 1988..... Count 45
- 7827 *Laotloe juglandis* (J.E. Smith)
May 18, 1988–July 13, 1990..... Count 22
- 7828 *Pachysphinx modesta* (Harr.)
June 5, 1992–June 15, 1988..... Count 2
- 7871 *Deidamia inscripta* (Harr.)
May 28, 1989–June 12, 1992..... Count 11
- 7885 *Darapsa myron* (Cram.)
June 1, 1988–July 24, 1989..... Count 10
- 7886 *Darapsa pholus* (Cram.)
June 6, 1991–July 4, 1989..... Count 3

Family NOTODONTIDAE

- 7895 *Clostera albosigna* Fitch
June 1–Aug. 24, 1990..... Count 21
- 7898 *Clostera strigosa* (Grt.)
June 1, 1988–Aug. 7, 1992..... Count 10
- 7901 *Clostera apicalis* (Wlk.)
July 19, 1991–Aug. 14, 1989..... Count 8
- 7902 *Datana ministra* (Drury)
May 30, 1991–July 15, 1988..... Count 9
- 7903 *Datana angusi* G. & R.
June 15, 1988–July 20, 1990..... Count 6
- 7904+ *Datana drexelii* Hy. Edw.
June 20, 1991–July 29, 1988..... Count 19

7906+	<i>Dataua contracta</i> Wlk. June 20, 1991–Aug. 7, 1989	Count 27
7915	<i>Nadata gibbosa</i> (J.E. Smith) May 28–Aug. 21, 1989	Count 291
7917	<i>Hyperaeschra georgica</i> (H.-S.) June 6–Aug. 2, 1991	Count 5
7919	<i>Peridea basitriens</i> (Wlk.) May 30, 1991–Aug. 24, 1990	Count 260
7920	<i>Peridea angulosa</i> (J.E. Smith) June 15, 1988–Sep. 4, 1992	Count 94
7922	<i>Phaosia rimosa</i> Pack. May 30, 1991–Aug. 9, 1990	Count 18
7924	<i>Odontostia elegans</i> (Stkr.) May 30, 1991–July 15, 1988	Count 4
7926	<i>Notodonta scitipennis</i> Wlk. July 15, 1988	Count 1
7929	<i>Nerice bidentata</i> Wlk. May 30, 1991–Aug. 21, 1989	Count 9
7930	<i>Ellida caniplaga</i> (Wlk.) May 30, 1991–July 31, 1989	Count 31
7931	<i>Glaphisia septentrionis</i> Wlk. June 5, 1992–Aug. 16, 1990	Count 18
7951+	<i>Symmerista albifrons</i> (J.E. Smith) May 30, 1991–Aug. 16, 1990	Count 142
7957	<i>Dasylophia anguina</i> (J.E. Smith) June 15, 1988	Count 1
7958	<i>Dasylophia thyatroides</i> (Wlk.) May 18, 1988–Aug. 24, 1990	Count 62
7974	<i>Misogada unicolor</i> (Pack.) June 26, 1989	Count 1
7975	<i>Macrurocampa marthesia</i> (Cram.) June 20, 1991–Aug. 9, 1990	Count 97
7994	<i>Heterocampa guttivitta</i> (Wlk.) May 18, 1988–Aug. 7, 1989	Count 369
7995	<i>Heterocampa bimaculata</i> Wlk. May 30, 1991–Aug. 24, 1990	Count 14
7998	<i>Lochnaeus manteo</i> Doubleday June 6, 1991–Aug. 5, 1988	Count 16
7999	<i>Lochnaeus bilineata</i> (Pack.) June 1, 1988–Aug. 21, 1989	Count 64
8005	<i>Schizura ipomoeae</i> Doubleday June 6, 1991–July 24, 1992	Count 8
8006	<i>Schizura badia</i> (Pack.) June 5, 1992–July 10, 1989	Count 3
8007	<i>Schizura unicornis</i> (J.E. Smith) May 30, 1991–Aug. 21, 1989	Count 57
8011	<i>Schizura leptinoides</i> (Grt.) May 30, 1991–July 8, 1988	Count 23
8012	<i>Oligocentria semirufescens</i> (Wlk.) June 6, 1991–July 4, 1989	Count 16
8017	<i>Oligocentria lignicolor</i> (Wlk.) July 31, 1989–Aug. 9, 1990	Count 3

Family ARCTIIDAE

8045.1	<i>Cranubidia pallida</i> Pack. July 31, 1989–Sep. 10, 1992	Count 10
8090	<i>Hypoprepia fucosa</i> Hbn. July 19, 1991	Count 1
8104	<i>Conachara cadburyi</i> Franc. June 5, 1992	Count 1

8107	<i>Haploa chymene</i> (Brown) July 5, 1991–Aug. 21, 1989	Count 146
8121+	<i>Holomehina aurantiaca</i> (Hbn.) June 6, 1991–July 31, 1992	Count 212
8129	<i>Pyrrharctia isabella</i> (J.E. Smith) June 6, 1991–Sep. 9, 1989	Count 18
8133	<i>Spilosoma latipennis</i> Stretch May 30, 1991–July 3, 1992	Count 10
8134	<i>Spilosoma congrua</i> Wlk. May 21, 1989–July 24, 1992	Count 208
8137	<i>Spilosoma virginica</i> (F.) May 28, 1989–Aug. 23, 1991	Count 54
8140	<i>Hyphantria cunea</i> (Drury) July 3, 1992	Count 3
8169+	<i>Apantesis phalerata</i> (Harr.) June 20, 1991–Sep. 9, 1989	Count 4
8197	<i>Apantesis virgo</i> (L.) July 29, 1988	Count 1
8203+	<i>Halysidota tessellaris</i> (J.E. Smith) May 30, 1991–Aug. 7, 1992	Count 909
8211	<i>Lophocampa caryae</i> Harr. May 30, 1991–June 15, 1988	Count 31
8214	<i>Lophocampa maculata</i> Harr. June 15, 1988	Count 1
8230	<i>Cycnia tenera</i> Hbn. July 4, 1989–Aug. 26, 1988	Count 5
8231	<i>Cycnia oregonensis</i> (Stretch) June 12, 1989	Count 1
8238	<i>Enchaetes egla</i> (Drury) June 22–July 29, 1988	Count 8
8262	<i>Ctenucha virginica</i> (Esp.) June 15, 1988	Count 1
8267	<i>Ciseps fulvicollis</i> (Hbn.) May 30, 1991–Sep. 9, 1989	Count 14

Family LYMANTRIIDAE

8294	<i>Dasychira vagans</i> (B. & McD.) July 20, 1990	Count 1
8296	<i>Dasychira basiflava</i> (Pack.) July 5, 1991–Aug. 16, 1990	Count 62
8297	<i>Dasychira matheri</i> Fgn. July 12, 1991	Count 16
8302	<i>Dasychira obliquata</i> (G. & R.) Aug. 9, 1990	Count 3
8304	<i>Dasychira plagiata</i> (Wlk.) July 6, 1990	Count 1
8314	<i>Orgyia definita</i> Pack. July 5, 1991–Sep. 24, 1988	Count 18
8316	<i>Orgyia leucostigma</i> (J.E. Smith) June 20, 1991–Sep. 21, 1990	Count 17
8318	<i>Lymantria dispar</i> (L.) July 12, 1991–Aug. 27, 1992	Count 407

Family NOCTUIDAE

8322	<i>Idia americalis</i> (Gn.) May 30, 1991–Sep. 25, 1992	Count 28
8323+	<i>Idia aemula</i> Hbn. May 30, 1991–Sep. 25, 1992	Count 116
8326	<i>Idia rotundalis</i> (Wlk.) June 27, 1991–Sep. 10, 1992	Count 255

8327	<i>Idia forbesi</i> (French) July 5, 1991–Aug. 16, 1990	Count 74	8411	<i>Colobochyla interpuncta</i> (Grt.) July 5–July 12, 1991	Count 3
8329	<i>Idia diminiendis</i> (B. & McD.) June 27, 1991–Aug. 14, 1989	Count 67	8412	<i>Melanomma auricinctaria</i> Grt. May 30, 1991–Aug. 21, 1989	Count 7
8333	<i>Idia denticulalis</i> (Harv.) June 20, 1991–Sep. 7, 1990	Count 5	8421	<i>Hypenodes fragilinea</i> (Sm.) Aug. 27, 1992	Count 2
8334	<i>Idia lubricalis</i> (Gey.) July 8, 1988–Sep. 9, 1989	Count 17	8426	<i>Dyspyralis illocata</i> Warr. July 12–July 19, 1991	Count 2
8338	<i>Phalaenophana pyramusalis</i> (Wlk.) June 12, 1989–Aug. 31, 1990	Count 18	8427	<i>Dyspyralis puncticosta</i> (Sm.) July 5, 1991–July 29, 1988	Count 37
8340	<i>Zanclognatha lituralis</i> (Hbn.) June 5–Aug. 27, 1992	Count 38	8428	<i>Dyspyralis nigella</i> (Stkr.) July 5, 1991–Aug. 9, 1990	Count 39
8345	<i>Zanclognatha laevigata</i> (Grt.) July 4, 1989–Sep. 4, 1992	Count 198	8441	<i>Bomolocha manalis</i> (Wlk.) June 8, 1988–Sep. 9, 1989	Count 56
8347	<i>Zanclognatha obscuripennis</i> (Grt.) Sep. 9, 1989	Count 1	8442	<i>Bomolocha baltimoralis</i> (Gn.) May 18, 1988–Sep. 21, 1990	Count 136
8348	<i>Zanclognatha pedipalis</i> (Gn.) Aug. 16, 1990–Aug. 27, 1992	Count 3	8443	<i>Bomolocha bijugalis</i> (Wlk.) July 8, 1988	Count 1
8349	<i>Zanclognatha protummulalis</i> (Wlk.) July 19, 1991–July 24, 1989	Count 2	8444	<i>Bomolocha palparia</i> (Wlk.) June 15, 1988–Aug. 23, 1991	Count 14
8351	<i>Zanclognatha cruralis</i> (Gn.) June 6, 1991–Aug. 24, 1990	Count 27	8445	<i>Bomolocha abalienalis</i> (Wlk.) June 1, 1988–Aug. 21, 1989	Count 9
8352+	<i>Zanclognatha jachusalis</i> (Wlk.) May 30, 1991–Sep. 14, 1990	Count 258	8446	<i>Bomolocha deceptalis</i> (Wlk.) June 12–Sep. 9, 1989	Count 25
8355	<i>Chytolita morbidalis</i> (Gn.) May 30, 1991–July 4, 1989	Count 83	8447	<i>Bomolocha madefactalis</i> (Gn.) June 26, 1989–Sep. 7, 1990	Count 10
8356	<i>Chytolita petrealis</i> Grt. June 5–June 26, 1992	Count 6	8448	<i>Bomolocha sordidula</i> (Grt.) June 15, 1988	Count 1
8357	<i>Macrochilo absorptalis</i> (Wlk.) July 4, 1989–July 8, 1988	Count 3	8452	<i>Bomolocha edictalis</i> (Wlk.) July 3, 1992	Count 1
8358	<i>Macrochilo litophora</i> (Grt.) June 27, 1991–July 24, 1989	Count 26	8465	<i>Plathypena scabra</i> (F.) May 30, 1991–Sep. 25, 1992	Count 54
8360	<i>Macrochilo orciferalis</i> (Wlk.) June 15, 1988–Sep. 9, 1989	Count 2	8479	<i>Spargaloma sexpunctata</i> Grt. May 30, 1991–Aug. 24, 1990	Count 9
8362	<i>Phalaenostola metonalis</i> (Wlk.) May 30, 1991–Sep. 10, 1992	Count 15	8491	<i>Ledaea perditalis</i> (Wlk.) May 30–Aug 16, 1991	Count 11
8363	<i>Phalaenostola eumelusalis</i> (Wlk.) July 8, 1988–Aug. 2, 1991	Count 6	8499	<i>Metalectra discalis</i> (Grt.) July 5, 1991–July 31, 1989	Count 8
8364	<i>Phalaenostola larentioides</i> Grt. July 15, 1988–July 20, 1990	Count 2	8500	<i>Metalectra quadrisignata</i> (Wlk.) Aug. 9, 1990	Count 1
8370	<i>Bleptina caradrinalis</i> Gn. July 4, 1989–July 12, 1991	Count 2	8514	<i>Scolecocampa liburna</i> (Gey.) June 20, 1991–Aug. 16, 1990	Count 84
8378	<i>Renia salusalis</i> (Wlk.) June 20, 1991–July 17, 1992	Count 5	8534	<i>Plusiodonta compressipalpis</i> Gn. July 5, 1991	Count 1
8379	<i>Renia factiosalis</i> (Wlk.) July 5, 1991–Sep. 7, 1990	Count 126	8536	<i>Calyptra canadensis</i> (Bethune) June 20, 1991–Aug. 19, 1988	Count 13
8381	<i>Renia discoloralis</i> Gn. June 26, 1989–Sep. 4, 1992	Count 117	8555	<i>Scoliopteryx libatrix</i> (L.) May 21, 1989–Aug. 9, 1990	Count 6
8386	<i>Renia adspersigillus</i> (Bosc) June 6, 1991–Sep. 7, 1990	Count 47	8587	<i>Panopoda rufimargo</i> (Hbn.) June 20, 1991–Aug. 5, 1988	Count 91
8387	<i>Renia sobrialis</i> (Wlk.) July 10, 1989–Aug. 7, 1992	Count 4	8588	<i>Panopoda carneicosta</i> Gn. July 8, 1988–July 24, 1992	Count 5
8393	<i>Lascoria ambigualis</i> Wlk. June 1, 1990–Aug. 23, 1991	Count 13	8641	<i>Drasteria grandirena</i> (Haw.) July 4, 1989	Count 1
8397	<i>Palthis angualis</i> (Hbn.) May 30, 1991–Sep. 9, 1989	Count 12	8697	<i>Zale minerea</i> (Gn.) May 28, 1992–July 8, 1988	Count 38
8398	<i>Palthis asopialis</i> (Gn.) May 30, 1991–Sep. 25, 1992	Count 32	8705	<i>Zale bethunei</i> (Sm.) June 22, 1988	Count 1
8404	<i>Rivula propinquialis</i> Gn. May 30–Sep. 13, 1991	Count 33	8716	<i>Zale unilineata</i> (Grt.) June 15, 1988	Count 2

8717	<i>Zale horrida</i> Hbn. May 30, 1991–Aug. 16, 1990	Count 3
8721	<i>Allotria elonympha</i> (Hbn.) June 15, 1988–Aug. 7, 1989	Count 8
8727	<i>Parallelia bistriaris</i> Hbn. May 30, 1991–Sep. 9, 1989	Count 58
8738+	<i>Caenurgina crassiuscula</i> (Haw.) July 24, 1992–Sep. 9, 1989	Count 3
8778	<i>Catocala habilis</i> Grt. Aug. 16, 1991–Sep. 25, 1992	Count 4
8779	<i>Catocala serena</i> Edw. July 20, 1990	Count 1
8785	<i>Catocala residua</i> Grt. Sep. 9, 1989	Count 1
8788	<i>Catocala relecta</i> Grt. Aug. 23, 1991–Sep. 25, 1992	Count 7
8792	<i>Catocala vidua</i> (J.E. Smith) Sep. 14, 1990	Count 1
8795	<i>Catocala palaeogama</i> Gn. Aug. 16, 1991–Sep. 14, 1990	Count 4
8797	<i>Catocala subnata</i> Grt. Aug. 16, 1990	Count 1
8798	<i>Catocala neogama</i> (J.E. Smith) Sep. 25, 1992	Count 1
8801	<i>Catocala ilia</i> (Cram.) July 5, 1991–Sep. 9, 1989	Count 15
8802	<i>Catocala cerogama</i> Gn. Aug. 5–Sep. 24, 1988	Count 20
8805	<i>Catocala unijuga</i> Wlk. Aug. 24, 1990	Count 1
8806	<i>Catocala parta</i> Gn. July 24, 1989–Aug. 3, 1990	Count 2
8832	<i>Catocala cara</i> Gn. Sep. 25, 1992	Count 1
8833	<i>Catocala concubens</i> Wlk. Sep. 4, 1992	Count 1
8857	<i>Catocala ultronia</i> (Hbn.) July 5, 1991–Sep. 9, 1989	Count 61
8858	<i>Catocala crataegi</i> Saund. July 12, 1991	Count 1
8863	<i>Catocala mira</i> Grt. July 5, 1991–Aug. 21, 1989	Count 21
8864	<i>Catocala grynea</i> (Cram.) July 5, 1991–Sep. 9, 1989	Count 28
8865	<i>Catocala praeclara</i> G. & R. July 12, 1991–July 31, 1989	Count 4
8867	<i>Catocala blandula</i> Hulst July 8, 1988–July 31, 1989	Count 9
8878	<i>Catocala amica</i> (Hbn.) Sep. 9, 1989	Count 1
8898	<i>Allagrapha aerea</i> (Hbn.) June 6, 1991–Sep. 7, 1990	Count 20
8899	<i>Pseudeva purpurigera</i> (Wlk.) June 15, 1988–July 17, 1989	Count 4
8905	<i>Eosphorapteryx thyatroides</i> (Gn.) July 24, 1989–Sep. 21, 1990	Count 4
8908	<i>Autographa precatonis</i> (Gn.) May 28–Sep. 25, 1992	Count 13
8924	<i>Anagrapha falcifera</i> (Kby.) May 30–July 26, 1991	Count 3
8955	<i>Marathyssa inficta</i> (Wlk.) June 15, 1988	Count 1
8956	<i>Marathyssa basalis</i> Wlk. May 21, 1989	Count 1
8957	<i>Paectes oculatrix</i> (Gn.) June 12, 1989–Aug. 24, 1990	Count 17
8970	<i>Baileya ophthalmica</i> (Gn.) May 21, 1989–July 8, 1988	Count 48
8971	<i>Baileya dormitans</i> (Gn.) May 30–July 19, 1991	Count 72
8972	<i>Baileya levitans</i> (Sm.) May 28, 1989–Aug. 3, 1990	Count 42
8973	<i>Baileya australis</i> (Grt.) June 1, 1988	Count 1
8983	<i>Meganola minuscula</i> (Zell.) May 21, 1989–July 19, 1991	Count 10
8983.1	<i>Meganola phylla</i> (Dyar) June 1, 1988–Aug. 2, 1991	Count 10
9037	<i>Hyperstrotia pervertens</i> (B. & McD.) May 30, 1991–Sep. 14, 1990	Count 47
9038	<i>Hyperstrotia villificans</i> (B. & McD.) July 12, 1991	Count 3
9040	<i>Hyperstrotia secta</i> (Grt.) July 19, 1991	Count 1
9046	<i>Lithocodia bellicula</i> Hbn. July 8, 1988	Count 1
9047	<i>Lithocodia muscosa</i> (Gn.) May 18, 1988–Aug. 23, 1991	Count 144
9048	<i>Lithocodia albidula</i> (Gn.) July 19–July 26, 1991	Count 2
9051	<i>Lithocodia musta</i> (G. & R.) July 29, 1988	Count 1
9053	<i>Pseudeustrotia carneola</i> (Gn.) May 30, 1991–Sep. 9, 1989	Count 85
9055.1	<i>Maliattha synochitis</i> (G. & R.) May 30, 1991–July 20, 1990	Count 40
9055.3	<i>Anterastria teratophora</i> (H.-S.) June 12, 1989	Count 1
9056	<i>Homophoberia cristata</i> Morr. July 8, 1988	Count 1
9057	<i>Homophoberia apicosa</i> (Haw.) May 30, 1991–Aug. 24, 1990	Count 20
9062	<i>Cerna cerintha</i> (Tr.) June 6, 1991–July 15, 1988	Count 8
9065	<i>Leuconycta dipteroides</i> (Gn.) June 1–July 15, 1988	Count 15
9066	<i>Leuconycta lepidula</i> (Grt.) July 12, 1991–Aug. 19, 1988	Count 2
9090	<i>Tarachidia candefacta</i> (Hbn.) July 15–Aug. 5, 1988	Count 2
9095	<i>Tarachidia erastrioides</i> (Gn.) June 1–July 15, 1988	Count 4
9185	<i>Colocasia propinquinella</i> (Grt.) May 21, 1989–July 12, 1991	Count 108
9189	<i>Charadra deridens</i> (Gn.) June 15, 1988–Aug. 2, 1991	Count 3
9193	<i>Raphia frater</i> Grt. May 30, 1991–July 31, 1989	Count 19
9200	<i>Acronicta americana</i> (Harr.) June 6, 1991–July 15, 1988	Count 22

9203	<i>Acronicta dactylina</i> Grt. July 24, 1992.....	Count 1
9207	<i>Acronicta imotata</i> Gn. July 17, 1989.....	Count 1
9225	<i>Acronicta vinnula</i> (Grt.) July 31, 1989.....	Count 1
9226	<i>Acronicta superans</i> Gn. May 21–June 12, 1989.....	Count 2
9227	<i>Acronicta lactifica</i> Sm. June 1, 1988–Aug. 2, 1991.....	Count 9
9229	<i>Acronicta hasta</i> Gn. May 28, 1989–Aug. 19, 1988.....	Count 45
9235	<i>Acronicta spinigera</i> Gn. May 28–Aug. 21, 1989.....	Count 198
9236	<i>Acronicta morula</i> G. & R. June 12, 1989–July 10, 1992.....	Count 4
9237	<i>Acronicta interrupta</i> Gn. May 30, 1991–June 12, 1989.....	Count 2
9238	<i>Acronicta lobeliae</i> Gn. June 12, 1989.....	Count 1
9242	<i>Acronicta exilis</i> Grt. May 30, 1991.....	Count 1
9243	<i>Acronicta ovata</i> Grt. June 26, 1989–July 15, 1988.....	Count 9
9244	<i>Acronicta modica</i> Wlk. July 8–July 15, 1988.....	Count 2
9245+	<i>Acronicta haesitata</i> (Grt.) May 30, 1991–July 20, 1990.....	Count 314
9246	<i>Acronicta clarescens</i> Gn. June 15, 1988.....	Count 2
9251	<i>Acronicta retardata</i> (Wlk.) May 30–July 19, 1991.....	Count 12
9261	<i>Acronicta impressa</i> Wlk. July 12, 1991–July 20, 1990.....	Count 2
9285	<i>Polygrammate hebraeicum</i> Hbn. May 30, 1991–Aug. 15, 1988.....	Count 38
9286	<i>Harrisinemma trisignata</i> (Wlk.) Aug. 5, 1988.....	Count 1
9301	<i>Eudryas grata</i> (F.) May 30, 1991–July 29, 1988.....	Count 51
9314	<i>Altypia octomaculata</i> (F.) June 22, 1988.....	Count 1
9328	<i>Apamea nigrrior</i> (Sm.) June 6, 1991.....	Count 1
9329	<i>Apamea cariosa</i> (Gn.) July 29, 1988.....	Count 1
9332	<i>Apamea vulgaris</i> (G. & R.) June 22, 1990–July 19, 1991.....	Count 5
9333	<i>Apamea lignicolora</i> (Gn.) July 13, 1990.....	Count 1
9348	<i>Apamea amputatrix</i> (Fitch) July 19, 1992.....	Count 1
9391	<i>Luperina passer</i> (Gn.) June 27, 1991.....	Count 1
9404	<i>Oligia modica</i> (Gn.) Aug. 9–Sep. 14, 1990.....	Count 23
9406	<i>Oligia fractilinea</i> (Grt.) July 12–Aug. 16, 1991.....	Count 14
9410	<i>Oligia crytora</i> (Franc.) June 29, 1990.....	Count 1
9419	<i>Oligia mactata</i> (Gn.) July 3–Sep. 25, 1992.....	Count 18
9427	<i>Meropleon diversicolor</i> (Morr.) Aug. 31, 1990.....	Count 1
9454	<i>Amphipoea velata</i> (Wlk.) June 20, 1991–July 21, 1992.....	Count 8
9466	<i>Papaipema cataphracta</i> (Grt.) Sep. 25, 1992.....	Count 1
9471	<i>Papaipema activorens</i> Hamp. Sep. 2, 1989–Sep. 25, 1992.....	Count 21
9483	<i>Papaipema inquaesita</i> (G. & R.) Aug. 19, 1988–Sep. 25, 1992.....	Count 20
9485	<i>Papaipema baptisiae</i> (Bird) Sep. 14–Sep. 21, 1990.....	Count 4
9503	<i>Papaipema rigida</i> (Grt.) Sep. 9, 1989.....	Count 1
9505	<i>Papaipema cerussata</i> (Grt.) Sep. 9, 1989–Sep. 25, 1992.....	Count 3
9509	<i>Papaipema unimoda</i> (Sm.) Aug. 31, 1990.....	Count 1
9520	<i>Achatodes zeae</i> (Harr.) July 12, 1991–Aug. 24, 1990.....	Count 3
9525	<i>Bellura obliqua</i> (Wlk.) May 30, 1991.....	Count 1
9526	<i>Bellura densa</i> (Wlk.) Aug. 7, 1989.....	Count 1
9545	<i>Euplexia benesimilis</i> McD. May 30, 1991–Sep. 7, 1990.....	Count 108
9546	<i>Phlogophora iris</i> Gn. June 22, 1988.....	Count 1
9547	<i>Phlogophora periculosa</i> Gn. Aug. 16–Sep. 14, 1990.....	Count 91
9549	<i>Enargia decolor</i> (Wlk.) July 24, 1992.....	Count 1
9550	<i>Enargia infumata</i> (Grt.) June 13, 1991–July 10, 1989.....	Count 19
9551	<i>Enargia mephisto</i> Franc. June 6, 1991–July 10, 1989.....	Count 15
9555	<i>Ipinorpha pleonectusa</i> Grt. July 31–Sep. 9, 1989.....	Count 11
9556	<i>Chytonix palliatricula</i> (Gn.) June 1, 1988–July 31, 1992.....	Count 105
9578	<i>Hyppa xylinoides</i> (Gn.) May 18, 1988–Sep. 2, 1989.....	Count 43
9582	<i>Nedra ramosula</i> (Gn.) Aug. 16, 1991.....	Count 1
9618	<i>Phosphila turbulenta</i> Hbn. July 5–July 12, 1991.....	Count 3
9631	<i>Callopietria mollissima</i> (Gn.) May 30, 1991–Sep. 9, 1989.....	Count 79
9633	<i>Callopietria cordata</i> (Ljungh) July 4, 1989.....	Count 1
9638	<i>Amphipyra pyramioides</i> Gn. May 21, 1989–Sep. 25, 1992.....	Count 123
9647	<i>Athetis miranda</i> (Grt.) Aug. 14, 1989.....	Count 1
9650	<i>Anorthodes tarda</i> (Gn.) June 4, 1989–Sep. 25, 1992.....	Count 27
9661	<i>Crambodes talidiformis</i> Gn. Aug. 27, 1992.....	Count 1

9662	<i>Balsa malana</i> (Fitch) June 15, 1988–Aug. 9, 1990.....	Count 11	10444+	<i>Leucania phragmatidicola</i> Gn. May 30, 1991–Sep. 4, 1992.....	Count 7
9663	<i>Balsa tristrigella</i> (Wlk.) May 30, 1991–July 4, 1989.....	Count 73	10446+	<i>Leucania multilinea</i> Wlk. July 19–Aug. 30, 1991.....	Count 15
9664	<i>Balsa labecula</i> (Grt.) June 1, 1990–July 29, 1988.....	Count 31	10447	<i>Leucania commoides</i> Gn. Aug. 7, 1989.....	Count 1
9666	<i>Spodoptera frugiperda</i> (J.E. Smith) Aug. 30, 1991.....	Count 1	10461+	<i>Leucania ursula</i> (Fbs.) May 30, 1991–Sep. 10, 1988.....	Count 36
9678	<i>Elaphria versicolor</i> (Grt.) June 15, 1988–July 10, 1989.....	Count 10	10495+	<i>Orthosia hibisci</i> (Gn.) May 21, 1989.....	Count 1
9681	<i>Elaphria festivoides</i> (Gn.) June 15, 1988–July 10, 1992.....	Count 4	10501	<i>Crocigrapha normani</i> (Grt.) May 18, 1988–June 5, 1992.....	Count 19
9689	<i>Perigea xanthioides</i> Gn. June 15, 1988–Sep. 9, 1989.....	Count 13	10521	<i>Morrisonia confusa</i> (Hbn.) May 18–June 15, 1988.....	Count 9
9696	<i>Condica vecors</i> (Gn.) May 30–Aug. 16, 1991.....	Count 16	10521.1	<i>Morrisonia latex</i> (Gn.) May 28, 1989–July 15, 1988.....	Count 39
9720	<i>Ogdoconta cinereola</i> (Gn.) May 30, 1991–Sep. 9, 1989.....	Count 16	10524	<i>Nephelodes minians</i> Gn. Aug. 27, 1992–Sep. 13, 1991.....	Count 19
9815	<i>Cosmia calami</i> (Harv.) July 5, 1991.....	Count 1	10532	<i>Homorthodes fufurata</i> (Grt.) June 27, 1991–July 24, 1992.....	Count 5
9818	<i>Amolita fessa</i> Grt. June 27, 1991–July 10, 1989.....	Count 3	10578	<i>Pseudorthodes vecors</i> (Gn.) June 5–Sep. 4, 1992.....	Count 120
9878	<i>Lithomoia germana</i> (Morr.) Sep. 6, 1991–Sep. 25, 1992.....	Count 4	10585	<i>Orthodes crenulata</i> (Butler) July 15, 1988–Aug. 30, 1991.....	Count 10
9886	<i>Lithophan patefacta</i> (Wlk.) Sep. 9, 1989.....	Count 1	10587	<i>Orthodes cynica</i> Gn. May 30, 1991–July 24, 1992.....	Count 561
9888	<i>Lithophane inominata</i> (Sm.) May 21, 1989–Sep. 21, 1990.....	Count 3	10589.1	<i>Orthodes goodelli</i> (Grt.) May 28–June 5, 1992.....	Count 3
9893	<i>Lithophane hemina</i> Grt. Sep. 25, 1992.....	Count 1	10627	<i>Tricholita signata</i> (Wlk.) July 26, 1991–Sep. 21, 1990.....	Count 19
9929	<i>Pyreferra hesperidago</i> (Gn.) May 21, 1989.....	Count 1	10663	<i>Agrotis ipsilon</i> (Hufn.) May 25, 1988–Sep. 25, 1992.....	Count 63
9952	<i>Eucliroedia pampina</i> (Gn.) Sep. 10, 1992.....	Count 1	10664	<i>Agrotis subterranea</i> (F.) July 12, 1991.....	Count 1
9957	<i>Samira bicolorago</i> (Gn.) Sep. 14, 1990–Sep. 25, 1992.....	Count 10	10674+	<i>Feltia subgothica</i> (Haw.) Aug. 7, 1989–Aug. 30, 1991.....	Count 7
9961	<i>Anathix ralla</i> (G. & R.) Aug. 16, 1990–Sep. 25, 1992.....	Count 137	10676	<i>Feltia herilis</i> (Grt.) Aug. 2, 1991–Sep. 4, 1992.....	Count 10
10200	<i>Cucullia asteroides</i> Gn. Aug. 19, 1988.....	Count 1	10793	<i>Euxoa scholastica</i> McD. July 15, 1988.....	Count 1
10276	<i>Polia inbrifera</i> (Gn.) June 6, 1991–July 10, 1989.....	Count 20	10891	<i>Ochropleura plecta</i> (L.) May 30, 1991–Sep. 10, 1988.....	Count 154
10288+	<i>Polia detracta</i> (Wlk.) May 30, 1991–Aug. 24, 1990.....	Count 686	10915	<i>Peridroma saucia</i> (Hbn.) Sep. 9, 1989.....	Count 1
10292	<i>Melanchra adjuncta</i> (Gn.) May 30, 1991–Sep. 9, 1989.....	Count 10	10917	<i>Diarsia rubifera</i> (Grt.) Aug. 9, 1990.....	Count 1
10299	<i>Lacania subijuncta</i> (G. & R.) June 4–Aug. 21, 1989.....	Count 4	10926	<i>Spaelotis clandestina</i> (Harr.) June 15, 1990.....	Count 1
10300	<i>Spiramater grandis</i> (Gn.) June 12, 1992–July 26, 1991.....	Count 2	10942.1+	<i>Xestia dolosa</i> Franc. May 30, 1991–Sep. 21, 1990.....	Count 354
10368	<i>Lacinipolia meditata</i> (Grt.) Aug. 7, 1992.....	Count 1	10943	<i>Xestia normaniana</i> (Grt.) Aug. 5, 1988–Sep. 25, 1992.....	Count 149
10397	<i>Lacinipolia renigera</i> (Steph.) June 12, 1992–Sep. 9, 1989.....	Count 14	10944	<i>Xestia smithii</i> (Snell.) Aug. 16, 1991–Sep. 25, 1992.....	Count 50
10405	<i>Lacinipolia lorea</i> (Gn.) May 30, 1991–July 8, 1988.....	Count 44	10950+	<i>Xestia bicarnea</i> (Gn.) Aug. 2–Sep. 13, 1991.....	Count 137
10436	<i>Aletia oxygala</i> (Grt.) May 30, 1991–Sep. 2, 1989.....	Count 5	10998	<i>Choeophora fungorum</i> G. & R. Sep. 13, 1991.....	Count 1
10438	<i>Pseudaletia unipuncta</i> (Haw.) May 21, 1989–Sep. 10, 1988.....	Count 49	11006	<i>Protolampra brunneicollis</i> (Grt.) June 22, 1988–Aug. 24, 1990.....	Count 44

11007+	<i>Eueretagrotis sigmoides</i> (Gn.)		11029+	<i>Abagrotis alternata</i> (Grt.)	
	July 12, 1991	Count 1		July 5, 1991–Sep. 25, 1992	Count 41
11010	<i>Heptagrotis phyllophora</i> (Grt.)		11068	<i>Helicoverpa zea</i> (Boddie)	
	June 15–July 15, 1988	Count 6		Sep. 9, 1989	Count 1

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CHECKLIST OF THE MOTHS OF RESOURCES CENTER, HIDDEN VALLEY METROPARK, LAKE COUNTY, OHIO (1988–1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Resources Center, Hidden Valley Metropark, in Lake County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988–1992) and includes 16,959 specimens representing 528 species. The study began in 1987 and continued through 1996, but only data for 1988–1992 are included here. The checklist is a historical record of the species that were present in 1988–1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after ten years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988–1992 is 7.19 and the Shannon-Wiener Evenness Index is 0.80. Two hundred thirty-five of the 528 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. The less abundant species at Resources Center are not less likely to be widespread than the more abundant species at Resources Center, except for the singletons. Five species of owl moths that were collected at Resources Center are of special interest in Ohio. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Introduction

The objective of this study was to document the population changes of native moths for ten years at several sites within the drainage basin of the Grand River in Trumbull, Ashtabula, and Lake Counties, Ohio, during gypsy moth invasion and control. This is the fifth in a series of checklists that tabulate the moths collected at each site during 1988–1992.

Over this same period, the population of the gypsy moth increased in the entire drainage basin. Pheromone trap catches of male gypsy moths increased at Resources Center from $33 \pm 7(7)$ per trap in 1987 [mean \pm standard error (number of traps)], to $69 \pm 24(4)$ in 1988, $276 \pm 35(4)$ in 1989, $105 \pm 20(4)$ in 1990, and $268 \pm 26(4)$ in 1991. Pheromone trapping was discontinued after 1991. Ultraviolet-light-trap catches of male gypsy moths also increased, from 2 in 1987, to 6 in 1988, 31 in 1989, 22 in 1990, 8 in 1991, and 35 in 1992, but noticeable defoliation was not observed at Resources Center.

The overall study provides baseline data on pre-outbreak moth diversity, as well as data on the impact of gypsy moth control agents.

Description of the Surveillance Site at Resources Center Metropark

Resources Center is composed of 15 ha of forest and is bordered by the Grand River to the south and a residential

area on the north. It is the northern section of Hidden Valley Metropark which spans the Grand River and totals 58 ha. Resources Center is situated on 0–6 m of Ashtabula Till over the Painesville Moraine (White, 1980, p. 6, Pl. 1).

The light trap at Resources Center was located in Madison Township in Lake County near the northern border of the Metropark on Palisade Drive at latitude $41^{\circ} 44' 31''$ N and longitude $81^{\circ} 03' 13''$ W (U.S. Geological Survey Thompson, Ohio, 7.5-minute quadrangle topographic map; Figure 1).

Resources Center is located approximately 21 km northeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

The composition of the canopy and understory was evaluated for the 2500 m² of forest centered on the surveillance trap (point-quarter technique, nine points; Cottam and Curtis, 1956; Cox, 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90 m at Resources. The importance values for the woody plants at the surveillance site at Resources Center are given in Table 1.

Hidden Valley Metropark contains five species of plants that appear on the 1994–1995 list of Rare Native

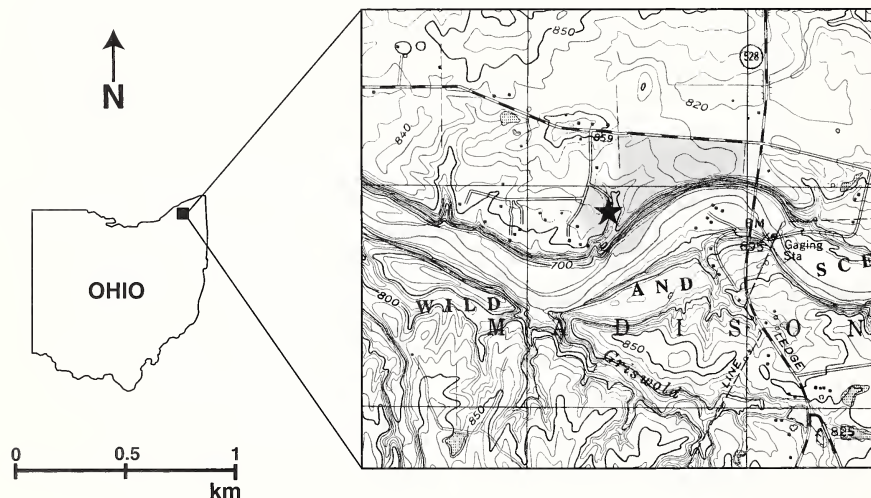


Figure 1. Map of the study area (adapted from the U.S. Geological Survey Thompson, Ohio, 7.5-minute quadrangle topographic map). Shaded area delineates Resources Center; star indicates position of surveillance trap within Hidden Valley Metropark.

Table 1. Importance values for woody plants at the surveillance site at Resources Center. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Woody Plant Species		Canopy	Understory
Ash	<i>Fraxinus</i> spp.	39	36
Maple, sugar	<i>Acer saccharum</i> Marsh.	32	86
Tuliptree	<i>Liriodendron tulipifera</i> L.	32	0
Pine, eastern white	<i>Pinus strobus</i> L.	28	0
Beech, American	<i>Fagus grandifolia</i> Ehrh.	26	0
Mulberry, red	<i>Morus rubra</i> L.	22	0
Basswood	<i>Tilia americana</i> L.	21	7
Oak, northern red	<i>Quercus rubra</i> L.	18	0
Hickory, shagbark	<i>Carya ovata</i> (Mill.) K. Koch	16	0
Hickory, bitternut	<i>Carya cordiformis</i> (Wang.) K. Koch	15	7
Hickory, mockernut	<i>Carya alba</i> (L.) Nutt. ex Ell.	15	0
Buckeye, Ohio	<i>Aesculus glabra</i> Willd.	10	0
Hemlock, eastern	<i>Tsuga canadensis</i> (L.) Carr.	7	85
Spruce, white	<i>Picea glauca</i> (Moench) Voss	7	10
Hop Hornbeam, eastern	<i>Ostrya virginiana</i> (Mill.) K. Koch	7	0
Walnut, black	<i>Juglans nigra</i> L.	7	0
Dogwood, flowering	<i>Cornus florida</i> L.	0	17
Spicebush	<i>Lindera benzoin</i> (L.) Blume	0	17
Lilac	<i>Syringa vulgaris</i> L.	0	12
Apple, domesticated	<i>Malus pumila</i> Miller	0	7
Grape, summer	<i>Vitis aestivalis</i> Michx.	0	7
Cedar	<i>Thuja occidentalis</i> L.	0	7

Ohio Plants (Quinn, 1995): one endangered plant, large-leaved mountain rice *Oryzopsis asperifolia* Michx.; and four potentially threatened plants, closed gentian *Gentiana clausa* Raf., Turk's-cap lily *Lilium superbum* L., sweet-scented indian plantain *Cacalia suaveolens* L., and Canadian buffalo-berry *Shepherdia canadensis* (L.) Nutt. (author citations according to Kartesz, 1994). These species were selected from a larger list of Resources species on deposit in the Herbarium at The Cleveland Museum of Natural History.

Surveillance Techniques

One Elliscope®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, usually from late May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were

computerized. All the specimens collected are deposited in the Insect Collection at The Cleveland Museum of Natural History.

Results and Discussion

A total of 16,959 specimens representing 528 species were collected in 1988–1992 (Appendix). Species were identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al. (1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodges et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 34 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1987 to 1996, is shown in Figure 2. In 1987 (not included in this checklist), 383 species were collected, and in 1996, after ten years, the total had reached 620 (1993–1996, also not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Resources Center and five years would have been a minimum. The species accumulation curve was still rising after ten years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: many fall, winter, and early spring moths may be missing because for 1989–1991, collecting was not begun until the end of May and collecting ended in September. For 1988 and 1992, collection began as early as March and continued through to November. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

Relative abundances of the 528 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among

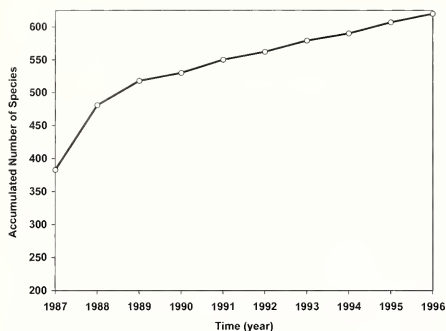


Figure 2. Plot of the annual accumulation of species collected at Resources Center, 1987–1996.

the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The Shannon-Wiener Diversity Index is 7.19 and the Shannon-Wiener Evenness Index is 0.80.

Almost nine percent of the total count was composed of lesser maple spanworm moth *Ilame pustularia* (6273). The next most abundant species was sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants. Following, in order of decreasing abundance, were: forest tent caterpillar moth *Malacosoma disstria* (7698)

whose larva feeds on trees and shrubs, especially aspens and maples; banded tussock moth *Halysidota tessellaris* (8203+) whose larva feeds on many deciduous trees; greater black-letter dart *Xestia dolosa* (10942.1+) whose larva feeds on apple, clover, maples, etc.; pale-marked angle *Semiothisa signaria* (6344+) whose larva feeds on many conifers; leafroller moth *Choristoneura fractivittana* (3632) whose larva feeds on apples, beeches, birches, etc.; common idia *Idia aemula* (8323+) whose larva feeds on dead leaves; esther moth *Hypagyrtis esther* (6655) whose larva feeds on pines; and common eupithecia, *Eupithecia miserulata* (7474+) whose larva feeds on asters, bayberry, and various deciduous trees.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 235 Resources Center species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988; 1990). Three explanations have been proposed (Krebs, 1994). First, the relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not

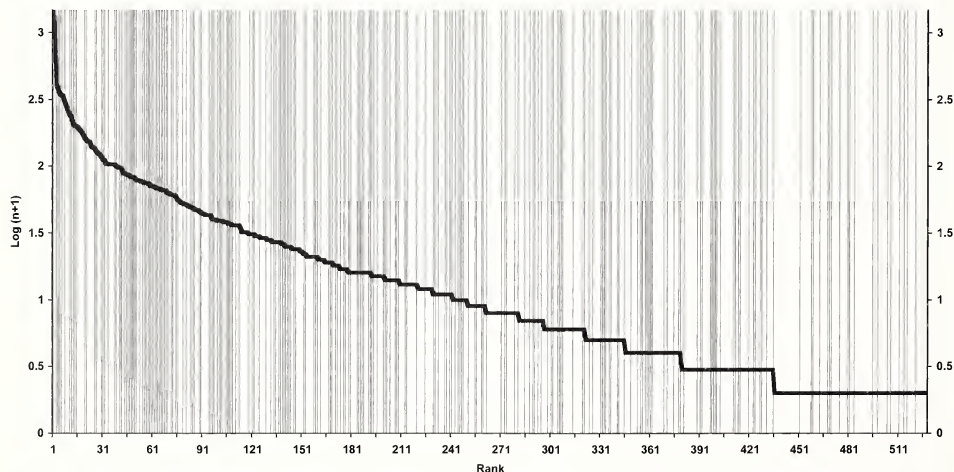


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Resources Center, 1988–1992.

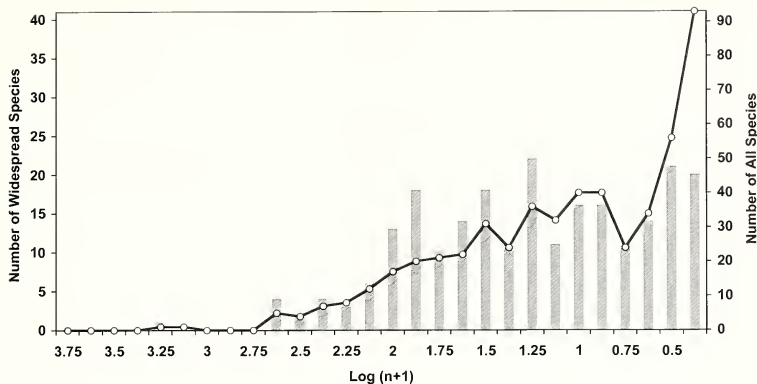


Figure 4. Correspondence between the total number of Resources Center species in an abundance interval (line, scale at right) and the number of widespread Resources Center species in the same abundance interval (bar, scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

exist, when abundance is viewed from the perspective of abundance at Resources Center. Of the 235 Resources Center species which are widespread in northeast Ohio, 105 had total counts of 10 or fewer at Resources Center.

Overall, there is a close correspondence between the number of widespread species in an abundance interval and the total number of species (Figure 4). Only the decrease in the proportion of widespread species in the singleton interval conforms to expectation. The 93 singleton species at Resources Center include only 20 widespread species whereas the 56 doubleton species include 21 widespread species.

Five species of owl moths collected at Resources Center are listed as being of special interest in Rings et al. (1992): *Idia laurenti* (8331) whose larval host is unrecorded; gray-banded zale *Zale squamularis* (8700) whose larva feeds on pine; large looper moth *Autographa ampla* (8923) whose larva feeds on trembling alder, birch, poplars, willows, and other woody plants; *Lithophane disposita* (9892) whose larva feeds on willows; and scurfy quaker *Homorthodes furfurata* (10532) whose larva feeds on maples. One species, *Eurotis occulta* (10929) whose larva feeds on birch and willow, is listed as status unknown.

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Appendix. Checklist of species collected at Resources Center, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family OECOPHORIDAE

- 882 *Agonopterix robinella* (Pack.)
July 8, 1988–Aug. 21, 1989 Count 2
- 951 *Machimia tentoriferella* Clem.
Sep. 30, 1988 Count 1
- 957 *Psilocorsis reflexella* Clem.
June 15, 1988–Aug. 21, 1992 Count 43
- 1014+ *Antaeotricha lencillana* (Zell.)
May 12, 1988–Aug. 27, 1992 Count 241
- 1046 *Callima argenticinctella* Clem.
July 24, 1989–Aug. 9, 1990 Count 11

Family COLEOPHORIDAE

- 1387 *Coleophora spissicornis* (Haw.)
June 6, 1991 Count 1

Family GELECHIIDAE

- 2295 *Trichoplus flavocostella* (Clem.)
July 4, 1989 Count 1

Family YPONOMEUTIDAE

- 2401 *Atteva punctella* (Cram.)
July 5, 1991–July 29, 1988 Count 7
- 2420 *Yponomeuta multipunctella* Clem.
June 20, 1991–July 24, 1989 Count 152

Family SESIIDAE

- 2554 *Synanthedon acerni* (Clem.)
June 12, 1989 Count 1

Family TORTRICIDAE

- 2863 *Hedya chionosema* (Zell.)
July 29, 1988 Count 1
- 3361 *Aucylis semiovana* (Zell.)
June 1–Aug. 19, 1988 Count 31
- 3503 *Croesia semipurpurana* (Kft.)
June 22, 1988 Count 1
- 3594 *Pandemis limitata* (Rob.)
June 8, 1990–Sep. 10, 1988 Count 38
- 3597 *Argyrotaenia velutinana* (Wlk.)
May 4, 1988–June 26, 1989 Count 4
- 3623 *Argyrotaenia quercifoliaria* (Fitch)
June 6, 1991–July 24, 1992 Count 52
- 3624 *Argyrotaenia alisellana* (Rob.)
June 6, 1991–July 3, 1992 Count 42
- 3625 *Argyrotaenia mariana* (Fern.)
May 2–June 1, 1988 Count 28
- 3632 *Choristoneura fractivittana* (Clem.)
May 30, 1991–Sep. 9, 1989 Count 332
- 3633 *Choristoneura parallela* (Rob.)
June 19, 1989–Sep. 7, 1990 Count 17

- 3635 *Choristoneura rosaceana* (Harr.)
June 12, 1992–Sep. 7, 1990 Count 172
- 3648 *Archips argyrospila* (Wlk.)
June 22, 1988 Count 3
- 3658 *Archips purpurana* (Clem.)
July 10, 1989 Count 1
- 3672 *Syndemis afflictana* (Wlk.)
May 12–May 18, 1988 Count 3
- 3686 *Clepsis melaleucana* (Wlk.)
May 30, 1991–June 26, 1989 Count 76
- 3720 *Sparganothis reticulatana* (Clem.)
July 4–Sep. 9, 1989 Count 12
- 3725 *Sparganothis pettitana* (Rob.)
June 20, 1991–July 24, 1989 Count 6
- 3748 *Amorbia humerosana* Clem.
June 15, 1988 Count 5

Family ZYGAENIDAE

- 4624 *Harrisina americana* (Guer.)
June 27, 1991 Count 1

Family LIMACODIDAE

- 4652 *Tortricidia testacea* Pack.
May 30, 1991–July 15, 1988 Count 87
- 4654 *Tortricidia flexuosa* (Grt.)
June 6, 1991–July 24, 1992 Count 124
- 4659 *Packardia geminata* (Pack.)
May 30, 1991–July 8, 1988 Count 15
- 4661 *Packardia elegans* (Pack.)
June 13, 1991 Count 1
- 4665 *Lithacodes fasciola* (H.-S.)
June 15, 1988–July 31, 1989 Count 37
- 4667 *Apoda y-inversum* (Pack.)
May 30, 1991–July 24, 1992 Count 18
- 4669 *Apoda biguttata* (Pack.)
June 15–July 22, 1988 Count 5
- 4671 *Prolimacodes badia* (Hbn.)
July 12, 1991 Count 2
- 4681 *Isa textula* (H.-S.)
June 22, 1990–July 12, 1991 Count 4
- 4685 *Adoneta spinuloides* (H.-S.)
July 29, 1988 Count 1
- 4697 *Euclea delphinii* (Bdv.)
June 22, 1988–July 17, 1992 Count 4

Family CRAMBIDAE

- 4703 *Gesneria centuriella* (D. & S.)
June 1, 1990–Aug. 21, 1989 Count 195
- 4748 *Mimroessa iccinsalis* (Wlk.)
July 12, 1991–July 31, 1989 Count 2

4774	<i>Petrophila bifascialis</i> (Rob.) July 24–Aug. 21, 1989	Count 11
4889	<i>Dicymolomia julianalis</i> (Wlk.) Aug. 2, 1991	Count 2
4897	<i>Evergestis pallidata</i> (Hufn.) June 15–Sep. 10, 1988	Count 7
4937	<i>Nascia acutella</i> (Wlk.) July 3, 1992–July 8, 1988	Count 2
4944	<i>Crocidophora serratissimalis</i> Zell. June 22–Sep. 10, 1988	Count 11
4945	<i>Crocidophora tubercularis</i> Led. June 20–July 26, 1991	Count 20
4949	<i>Ostrinia nubilalis</i> (Hbn.) May 30–Sep. 13, 1991	Count 65
4950	<i>Fumibotys fumalis</i> (Gn.) Aug. 7, 1992–Aug. 21, 1989	Count 2
4951	<i>Perispasta caecularis</i> Zell. June 26, 1992–Aug. 16, 1991	Count 3
4953a	<i>Phlyctaenia coronata tertialis</i> (Gn.) July 1, 1988–Aug. 14, 1989	Count 4
4962	<i>Hahncappsa marculenta</i> (G. & R.) June 1–July 15, 1988	Count 7
5040	<i>Pyrausta bicoloralis</i> (Gn.) June 6, 1991–Sep. 9, 1989	Count 9
5071	<i>Pyrausta acronialis</i> (Wlk.) June 5, 1992–Aug. 19, 1988	Count 12
5079	<i>Udea rubigalis</i> (Gn.) May 30, 1991–Oct. 10, 1992	Count 102
5142	<i>Diacne elealis</i> (Wlk.) May 21–Aug. 14, 1989	Count 19
5156	<i>Nonophila nearctica</i> Mun. July 5, 1991–Sep. 9, 1989	Count 7
5159	<i>Desmia funeralis</i> (Hbn.) June 1, 1988–Sep. 7, 1990	Count 82
5182	<i>Blepharomastix ranalis</i> (Gn.) July 5, 1991–July 13, 1990	Count 4
5226	<i>Palpita magniferalis</i> (Wlk.) May 30, 1991–Aug. 27, 1992	Count 102
5228	<i>Polygrammodes flavidalis</i> (Gn.) June 22, 1988–July 26, 1991	Count 5
5241	<i>Pantograph linata</i> (G. & R.) June 20, 1991–Sep. 9, 1989	Count 128
5272	<i>Herpetogramma bipunctalis</i> (F.) June 15–Aug. 19, 1988	Count 23
5275	<i>Herpetogramma perxtalis</i> (Led.) July 4–Aug. 21, 1989	Count 22
5280	<i>Herpetogramma aeglealis</i> (Wlk.) June 20–Aug. 2, 1991	Count 18
5362+	<i>Crambus agitatellus</i> Clem. May 30, 1991–Sep. 2, 1989	Count 1035
5403	<i>Agriphila vulgiragella</i> (Clem.) Sep. 10, 1992	Count 2
5413	<i>Pediasia trisecta</i> (Wlk.) July 26, 1991	Count 1
5464	<i>Urola nivalis</i> (Drury) June 27–Aug. 30, 1991	Count 27

Family PYRALIDAE

5518	<i>Aglossa cupriua</i> Zell. June 6–Aug. 30, 1991	Count 98
5524	<i>Hypsopygia costalis</i> (F.) July 3, 1992–Sep. 10, 1988	Count 10
5532	<i>Herculia infimbrialis</i> Dyar July 3, 1992–Aug. 21, 1989	Count 5
5533	<i>Herculia olinalis</i> (Gn.) July 8, 1988–July 24, 1989	Count 3
5552	<i>Galasa nigrinodis</i> (Zell.) June 20–July 5, 1991	Count 2
5556	<i>Tosale oviplagalis</i> (Wlk.) July 13, 1990	Count 2
5571	<i>Condylolomia participalis</i> Grt. June 20, 1991–July 27, 1990	Count 42
5577	<i>Epipaschia superatalis</i> Clem. July 8, 1988	Count 1
5622	<i>Galleria mellonella</i> (L.) Aug. 21–Sep. 9, 1989	Count 3
5997	<i>Euzophera ostricorella</i> Hulst June 15, 1988–July 12, 1991	Count 4
6053	<i>Peoria approximella</i> (Wlk.) July 4, 1989–Sep. 30, 1988	Count 4

Family THYRIDIDAE

6079	<i>Dysodia granulata</i> (Neum.) Aug. 21, 1989	Count 12
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Family THYATIRIDAE

6240	<i>Euthyatira pudens</i> (Gn.) May 12–May 18, 1988	Count 2
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Family DREPANIDAE

6251	<i>Drepana arcuata</i> Wlk. July 10, 1989	Count 1
6253	<i>Eudeilinia herminata</i> (Gn.) May 30–July 12, 1991	Count 2
6255	<i>Oreta rosea</i> (Wlk.) June 22, 1988–Sep. 7, 1990	Count 5

Family GEOMETRIDAE

6261	<i>Helionata cycladata</i> G. & R. May 30, 1991–June 22, 1988	Count 2
6270	<i>Protitame virginialis</i> (Hulst) June 15–July 22, 1988	Count 4
6273	<i>Itame pustularia</i> (Gn.) June 20, 1991–Sep. 9, 1989	Count 1480
6299	<i>Itame coartaria</i> (Hulst) June 22, 1988–July 10, 1992	Count 3
6335+	<i>Semiothisa aequiferaria</i> (Wlk.) June 12–Sep. 10, 1988	Count 65
6340	<i>Semiothisa minorata</i> (Pack.) May 30, 1991–Aug. 27, 1992	Count 43
6342	<i>Semiothisa bisignata</i> (Wlk.) June 15–Sep. 30, 1988	Count 54
6344+	<i>Semiothisa signaria</i> (Hbn.) May 4, 1988–Sep. 14, 1990	Count 340
6386	<i>Semiothisa ocellinata</i> (Gn.) June 15–Aug. 26, 1988	Count 51

6405	<i>Semiothisa gnophosaria</i> (Gn.) July 8, 1988–Aug. 2, 1991	Count 4	6797	<i>Ennomos magnaria</i> Gn. July 19, 1991–Oct. 27, 1988	Count 13
6583	<i>Anacamptodes ephyraia</i> (Wlk.) June 20, 1991–Aug. 3, 1990	Count 89	6798	<i>Ennomos subsignaria</i> (Hbn.) June 13, 1991–Aug. 7, 1989	Count 103
6584	<i>Anacamptodes humaria</i> (Gn.) July 8, 1988–Aug. 2, 1991	Count 7	6819	<i>Metanema inatomaria</i> Gn. June 6, 1991–July 8, 1988	Count 2
6586	<i>Anacamptodes defectaria</i> (Gn.) July 31, 1989	Count 1	6823	<i>Metarranthis angularia</i> B. & McD. June 22, 1988	Count 1
6588	<i>Iridopsis larvaria</i> (Gn.) May 30–Aug. 16, 1991	Count 12	6825	<i>Metarranthis indeclinata</i> (Wlk.) June 5–June 19, 1992	Count 10
6590	<i>Anavitrinella pampinaria</i> (Gn.) May 21, 1989–Sep. 10, 1988	Count 37	6826	<i>Metarranthis hypocharia</i> (H.-S.) June 6, 1991–July 3, 1992	Count 45
6597	<i>Ectropis crepuscularia</i> (D. & S.) May 4, 1988–Oct. 10, 1992	Count 60	6835	<i>Cepphis armataria</i> (H.-S.) June 15, 1988–July 10, 1989	Count 3
6598	<i>Protoboammia porcelaria</i> (Gn.) Sep. 13, 1991	Count 1	6836	<i>Anagoga occidentaria</i> (Wlk.) May 12, 1988–Aug. 14, 1989	Count 4
6599	<i>Epimecis hortaria</i> (F.) May 4, 1988–Aug. 16, 1990	Count 21	6838+	<i>Probole anticaria</i> (H.-S.) May 28, 1992–July 31, 1989	Count 62
6620+	<i>Melanolophia canadaria</i> (Gn.) May 4, 1988–Aug. 27, 1992	Count 68	6840	<i>Plagodis serinaria</i> H.-S. May 28–June 26, 1989	Count 86
6638	<i>Eufidonia notataria</i> (Wlk.) May 21, 1989–June 15, 1988	Count 60	6841	<i>Plagodis kuetzingi</i> (Grt.) June 1, 1990–June 5, 1992	Count 5
6640a	<i>Biston betularia cognataria</i> (Gn.) June 15–July 15, 1988	Count 2	6842	<i>Plagodis phlogosaria</i> (Gn.) June 20, 1991–Aug. 14, 1989	Count 29
6654	<i>Hypagyrtis unipunctata</i> (Haw.) June 6, 1991–Sep. 7, 1990	Count 13	6843	<i>Plagodis fervidaria</i> (H.-S.) May 12, 1988	Count 4
6655	<i>Hypagyrtis esther</i> (Barnes) May 30–Sep. 13, 1991	Count 282	6844	<i>Plagodis alcoalaria</i> (Gn.) May 12, 1988–Aug. 7, 1989	Count 65
6656	<i>Hypagyrtis piniata</i> (Pack.) May 12, 1988–June 20, 1991	Count 2	6863	<i>Caripeta divisata</i> Wlk. June 20, 1991–Aug. 26, 1988	Count 46
6660	<i>Phigalia strigataria</i> (Minot) Mar. 23–May 4, 1988	Count 7	6884	<i>Besma endropiaria</i> (G. & R.) May 28–Sep. 4, 1992	Count 60
6662	<i>Paleacrita vernata</i> (Peck) Mar. 23, 1988	Count 1	6885	<i>Besma quercivoraria</i> (Gn.) May 12, 1988–Sep. 2, 1989	Count 23
6665	<i>Erannis tiliaria</i> (Harr.) Nov. 3–Nov. 21, 1992	Count 13	6888	<i>Lambdina fiscellaria</i> (Gn.) June 1, 1988–Oct. 23, 1992	Count 8
6667	<i>Lomographa vestaliata</i> (Gn.) May 30, 1991–July 8, 1988	Count 39	6894a	<i>Lambdina fervidaria athasaria</i> (Wlk.) May 18, 1988	Count 1
6668	<i>Lomographa glomeraria</i> (Grt.) May 4, 1988–May 14, 1989	Count 8	6906	<i>Nepytia canosaria</i> (Wlk.) May 21, 1989–Oct. 27, 1988	Count 20
6677	<i>Cabera erythemaria</i> Gn. May 30, 1991–Aug. 27, 1992	Count 11	6909	<i>Nepytia pellucidaria</i> (Pack.) Oct. 10, 1992	Count 13
6720	<i>Lytrosia unitaria</i> (H.-S.) June 6, 1991–July 10, 1989	Count 26	6912	<i>Sicya macularia</i> (Harr.) June 22, 1990–July 10, 1989	Count 28
6724	<i>Euchlaena serrata</i> (Drury) July 8, 1988	Count 1	6941	<i>Eusarca confusaria</i> Hbn. June 5, 1992–Sep. 10, 1988	Count 35
6725	<i>Euchlaena muzaria</i> (Wlk.) June 6, 1991–June 26, 1989	Count 13	6963	<i>Tetracis crocallata</i> Gn. June 15–July 8, 1988	Count 3
6729	<i>Euchlaena johnsonaria</i> (Fitch) July 19, 1991–Aug. 24, 1990	Count 4	6964	<i>Tetracis cachexiata</i> Gn. May 30, 1991–July 3, 1992	Count 96
6739	<i>Euchlaena irvaria</i> (B. & McD.) June 6, 1991–June 26, 1989	Count 6	6965	<i>Eugonobapta nivosaria</i> (Gn.) June 27, 1991–July 17, 1992	Count 31
6740+	<i>Xanthotype urticaria</i> Swett May 30, 1991–Aug. 16, 1990	Count 10	6966	<i>Eitrapela clemataria</i> (J.E. Smith) May 4, 1988–Aug. 7, 1992	Count 42
6753+	<i>Pero honestaria</i> (Wlk.) May 4, 1988–Aug. 21, 1989	Count 70	6982	<i>Prochoerodes transversata</i> (Drury) June 20, 1991–Oct. 10, 1992	Count 51
6796	<i>Campea perlata</i> (Gn.) May 30, 1991–Sep. 25, 1992	Count 198	6987	<i>Antepione thisoaria</i> (Gn.) July 12, 1991–July 31, 1989	Count 4

7009	<i>Nematocampa limbata</i> (Haw.) June 20, 1991–Aug. 24, 1990	Count 28
7046+	<i>Nemoria bistriaria</i> Hbn. July 5, 1991–Aug. 27, 1992	Count 36
7047	<i>Nemoria rubrifrontaria</i> (Pack.) June 15, 1988	Count 4
7048	<i>Nemoria mimosaria</i> (Gn.) June 1, 1988–June 12, 1989	Count 7
7053	<i>Dichorda iridaria</i> (Gn.) June 12, 1989–Aug. 7, 1992	Count 4
7058	<i>Synchlora aerata</i> (F.) June 22, 1988–Sep. 13, 1991	Count 5
7071	<i>Chlorochlanys chlorolencaria</i> (Gn.) May 4, 1988–July 24, 1989	Count 20
7132	<i>Plenophrucha insularia</i> (Gn.) June 15, 1988–Sep. 9, 1989	Count 35
7136	<i>Cyclophora packardii</i> (Prout) June 5, 1992–July 5, 1991	Count 2
7139	<i>Cyclophora pendulinaria</i> (Gn.) June 1, 1988–Sep. 9, 1989	Count 13
7146	<i>Haematopsis grataria</i> (F.) July 10, 1992	Count 1
7157	<i>Scopula cacuminaria</i> (Morr.) June 20, 1991–July 24, 1992	Count 3
7159	<i>Scopula limboundata</i> (Haw.) June 12, 1992–Aug. 9, 1990	Count 74
7169	<i>Scopula inductata</i> (Gn.) July 12, 1991–Aug. 7, 1992	Count 7
7189	<i>Dysstroma hersiliata</i> (Gn.) June 8, 1988	Count 1
7196+	<i>Enlithis diversilineata</i> (Hbn.) July 27, 1991–Sep. 9, 1989	Count 21
7236+	<i>Hydriomena renunciata</i> (Wlk.) May 12–June 22, 1988	Count 14
7290	<i>Coryphista meadii</i> (Pack.) Aug. 21, 1989	Count 1
7292	<i>Hydria prunivora</i> (Fgn.) June 1, 1988	Count 1
7307	<i>Mesolenca ruficollata</i> (Gn.) July 29, 1988	Count 1
7329	<i>Anticlea vasilata</i> Gn. May 4, 1988	Count 1
7368	<i>Xanthorhoe labradorensis</i> (Pack.) June 26, 1989–Sep. 25, 1992	Count 7
7388	<i>Xanthorhoe ferrugata</i> (Cl.) Aug. 5, 1988–Aug. 16, 1991	Count 2
7390	<i>Xanthorhoe lacustrata</i> (Gn.) June 13, 1991–Sep. 9, 1989	Count 16
7399a	<i>Euphyia mngulata intermediata</i> (Gn.) June 6, 1991–Sep. 9, 1989	Count 10
7414	<i>Orthonama obspitata</i> (F.) May 4, 1988–Nov. 21, 1992	Count 62
7416	<i>Orthonama centrostrigaria</i> (Woll.) June 8, 1990–Aug. 25, 1992	Count 74
7422	<i>Hydrelia inornata</i> (Hulst) June 1, 1988–Aug. 14, 1989	Count 6
7430	<i>Trichodezia albovittata</i> (Gn.) June 22–Aug. 5, 1988	Count 2

7440	<i>Eubaphe medica</i> (Wlk.) June 6, 1991–July 17, 1989	Count 11
7445	<i>Horisme intestinata</i> (Gn.) June 8, 1990–Sep. 2, 1989	Count 8
7474+	<i>Enpithecia miserulata</i> Grt. Mar. 23–Oct. 16, 1988	Count 259
7638	<i>Cladara anguilineata</i> (G. & R.) May 12, 1988–May 21, 1989	Count 22
7640	<i>Lobophora nivigerata</i> Wlk. June 5, 1992	Count 1
7645	<i>Heterophleps refusaria</i> (Wlk.) June 22, 1988	Count 1
7647	<i>Heterophleps triguttaria</i> H.-S. July 8, 1988	Count 1
7648	<i>Dyspteris abortivaria</i> (H.-S.) July 12, 1991	Count 1

Family MIMALLONIDAE

7659	<i>Lacosoma chiridota</i> Grt. May 30, 1991	Count 1
7662	<i>Cicinnus melsheimeri</i> (Harr.) June 15, 1988–June 26, 1989	Count 5

Family APATELODIDAE

7663	<i>Apateles torrefacta</i> (J.E. Smith) June 22–July 8, 1988	Count 5
7665	<i>Olceclostera angelica</i> (Grt.) June 6, 1991–July 17, 1992	Count 5

Family LASIOCAMPIDAE

7670	<i>Tolyte velleda</i> (Stoll) July 12, 1991–Oct. 10, 1992	Count 15
7673	<i>Tolyte laricis</i> (Fitch) July 5, 1991–Sep. 14, 1990	Count 77
7698	<i>Malacosoma dissitia</i> Hbn. June 20, 1991–July 24, 1989	Count 405
7701	<i>Malacosoma americanum</i> (F.) June 6, 1991–July 17, 1989	Count 96

Family SATURNIIDAE

7715	<i>Dryocampa rubicanda</i> (F.) May 30, 1991–July 24, 1992	Count 12
7746	<i>Automeris io</i> (F.) June 1–July 22, 1988	Count 5
7757	<i>Antheraea polyphemus</i> (Cram.) July 12, 1991	Count 2
7758	<i>Actias luna</i> (L.) May 21, 1989–July 15, 1988	Count 9
7764	<i>Callosamia promethea</i> (Drury) June 27, 1991–July 8, 1988	Count 2

Family SPHINGIDAE

7787	<i>Ceratonia undulosa</i> (Wlk.) June 29–July 20, 1990	Count 2
7802	<i>Sphinx chersis</i> (Hbn.) June 15, 1988	Count 1
7824	<i>Paonias excaecatus</i> (J.E. Smith) June 1–July 29, 1988	Count 14
7825	<i>Paonias myops</i> (J.E. Smith) June 5, 1992–July 22, 1988	Count 3

7827	<i>Laothoe juglandis</i> (J.E. Smith) May 28, 1989–July 15, 1988	Count 9
7828	<i>Pachysphinx modesta</i> (Harr.) July 3, 1992	Count 1
7871	<i>Deidamia inscripta</i> (Harr.) May 28, 1989	Count 1
7885	<i>Darapsa myron</i> (Cram.) June 15–July 29, 1988	Count 6
7886	<i>Darapsa pholus</i> (Cram.) July 19, 1991	Count 1

Family NOTODONTIDAE

7895	<i>Clostera albosigma</i> Fitch July 4–July 24, 1989	Count 2
7896	<i>Clostera inclusa</i> (Hbn.) May 12, 1988	Count 3
7898	<i>Clostera strigosa</i> (Grt.) May 21, 1989–July 19, 1991	Count 3
7901	<i>Clostera apicalis</i> (Wlk.) May 28, 1992–Aug. 3, 1990	Count 3
7902	<i>Datana ministra</i> (Drury) June 6, 1991–July 22, 1988	Count 7
7903	<i>Datana angustii</i> G. & R. July 13, 1990	Count 1
7906+	<i>Datana contracta</i> Wlk. July 17–July 24, 1989	Count 3
7915	<i>Nadata gibbosa</i> (J.E. Smith) May 12, 1988–Aug. 27, 1992	Count 109
7917	<i>Hyperaeschra georgica</i> (H.-S.) May 4, 1988–July 31, 1989	Count 18
7919	<i>Peridea basitriens</i> (Wlk.) May 12, 1988–Aug. 24, 1990	Count 84
7920	<i>Peridea angulosa</i> (J.E. Smith) June 4, 1989–Aug. 27, 1992	Count 67
7922	<i>Pheosia rimosa</i> Pack. June 27, 1991–Aug. 26, 1988	Count 3
7924	<i>Odontotia elegans</i> (Stkr.) May 30, 1991–July 15, 1988	Count 2
7929	<i>Nerice bidentata</i> Wlk. July 17, 1989–Aug. 9, 1990	Count 5
7930	<i>Ellida caniplaga</i> (Wlk.) May 4, 1988–July 27, 1990	Count 44
7931	<i>Gluphisia septentrionis</i> Wlk. May 12, 1988–July 31, 1989	Count 4
7936	<i>Furcula borealis</i> (Guer.-Meneville) July 19, 1991–Aug. 16, 1990	Count 3
7951+	<i>Symmerista albifrons</i> (J.E. Smith) May 30, 1991–Aug. 27, 1992	Count 42
7958	<i>Dasylophia thyatiroides</i> (Wlk.) May 12, 1988–July 31, 1989	Count 3
7974	<i>Misogada unicolor</i> (Pack.) July 19, 1991	Count 1
7975	<i>Macrurocampa marthesia</i> (Cram.) June 20–Aug. 23, 1991	Count 35
7994	<i>Heterocampa guttivitta</i> (Wlk.) May 12, 1988–Aug. 21, 1989	Count 117
7995	<i>Heterocampa biundata</i> Wlk. June 12, 1989	Count 1

7998	<i>Lochnaenus manteo</i> Doubleday July 10, 1989–Aug. 5, 1988	Count 17
7999	<i>Lochnaenus bilineata</i> (Pack.) June 6, 1991–Aug. 21, 1989	Count 25
8005	<i>Schizura iponoeae</i> Doubleday July 22, 1988–July 31, 1989	Count 2
8007	<i>Schizura umicornis</i> (J.E. Smith) May 30, 1991–Aug. 21, 1989	Count 24
8011	<i>Schizura leptinoides</i> (Grt.) June 15–Aug. 5, 1988	Count 23
8012	<i>Oligoceutria semirufescens</i> (Wlk.) June 27, 1991–July 13, 1990	Count 4

Family ARCTIIDAE

8045.1	<i>Crambidia pallida</i> Pack. July 12, 1991–Aug. 27, 1992	Count 7
8104	<i>Comachara cadburyi</i> Franc. June 5, 1992	Count 1
8107	<i>Haploa clymene</i> (Brown) July 12, 1991–Aug. 7, 1992	Count 23
8121	<i>Holomelina aurantiaca</i> (Hbn.) June 20, 1991–Aug. 21, 1989	Count 122
8129	<i>Pyrharcia isabella</i> (J.E. Smith) June 28, 1992–Sep. 9, 1989	Count 17
8133	<i>Spilosoma latipennis</i> Stretch May 30, 1991–July 3, 1992	Count 12
8134	<i>Spilosoma congrua</i> Wlk. May 12, 1988–July 17, 1992	Count 157
8137	<i>Spilosoma virginica</i> (F.) May 30, 1991–Aug. 21, 1989	Count 38
8156	<i>Phragmatobia fuliginosa</i> (L.) July 5, 1991	Count 1
8169+	<i>Apantesis phalerata</i> (Harr.) May 28, 1992–Aug. 31, 1990	Count 37
8197	<i>Apantesis virgo</i> (L.) July 5, 1991–July 24, 1989	Count 7
8203+	<i>Halysidota tessellaris</i> (J.E. Smith) June 6, 1991–Aug. 7, 1992	Count 375
8211	<i>Lophocampa caryae</i> Harr. May 30, 1991–June 22, 1988	Count 19
8230	<i>Cynia tenera</i> Hbn. June 19–July 17, 1989	Count 13
8231	<i>Cynia oregonensis</i> (Stretch) May 30, 1991–July 29, 1988	Count 4
8238	<i>Euchaetes egle</i> (Drury) June 6, 1991–July 15, 1988	Count 6
8267	<i>Ciseps fulvicollis</i> (Hbn.) June 15, 1988–Sep. 9, 1989	Count 52

Family LYMANTRIIDAE

8296	<i>Dasychira basiflava</i> (Pack.) June 22, 1988–Aug. 7, 1992	Count 5
8302	<i>Dasychira obliquata</i> (G. & R.) July 10, 1989	Count 1
8304	<i>Dasychira plagiata</i> (Wlk.) June 20, 1991–July 10, 1992	Count 3
8314	<i>Orgyia definita</i> Pack. June 20, 1991–Sep. 21, 1990	Count 5

- 8316 *Orgyia leucostigma* (J.E. Smith)
June 27–Aug. 2, 1991 Count 3
- 8318 *Lymantria dispar* (L.)
July 5, 1991–Aug. 27, 1992 Count 102

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- 8322 *Idia americalis* (Gn.)
June 5–Oct. 10, 1992 Count 103
- 8323+ *Idia aemula* Hbn.
May 30, 1991–Oct. 23, 1992 Count 301
- 8326 *Idia rotundalis* (Wlk.)
June 27, 1991–Sep. 4, 1992 Count 187
- 8327 *Idia forbesi* (French)
July 5, 1991–Aug. 27, 1992 Count 152
- 8329 *Idia diminuendis* (B. & McD.)
July 5, 1991–Aug. 27, 1992 Count 137
- 8330 *Idia scobialis* (Grt.)
July 17–July 31, 1989 Count 6
- 8331 *Idia laurenti* (Sm.)
July 13–Aug. 16, 1990 Count 2
- 8334 *Idia lubricalis* (Gey.)
June 20, 1991–Aug. 27, 1992 Count 26
- 8338 *Phalaenophana pyramusalis* (Wlk.)
June 1–Sep. 10, 1988 Count 13
- 8340 *Zanclognatha lituralis* (Hbn.)
June 26, 1992–Aug. 14, 1989 Count 33
- 8345 *Zanclognatha laevigata* (Grt.)
June 20, 1991–Aug. 27, 1992 Count 50
- 8347 *Zanclognatha obscuripennis* (Grt.)
June 29, 1990 Count 1
- 8348 *Zanclognatha pedipalis* (Gn.)
June 12–Sep. 2, 1989 Count 19
- 8349 *Zanclognatha protumnusalis* (Wlk.)
July 5, 1991–Sep. 9, 1989 Count 5
- 8351 *Zanclognatha cruralis* (Gn.)
June 15, 1988–July 24, 1989 Count 14
- 8352+ *Zanclognatha jaccusalis* (Wlk.)
June 20, 1991–Sep. 30, 1988 Count 181
- 8355 *Chytolita morbidalis* (Gn.)
May 30, 1991–July 10, 1992 Count 78
- 8357.1 *Macrochilo hypocritalis* Fgn.
June 22, 1988–June 29, 1990 Count 2
- 8358 *Macrochilo litophora* (Grt.)
June 15, 1988–July 24, 1989 Count 20
- 8360 *Macrochilo orciferalis* (Wlk.)
June 15, 1988 Count 1
- 8362 *Phalaenostola metonalis* (Wlk.)
May 30, 1991–Sep. 4, 1992 Count 10
- 8363 *Phalaenostola eumehsalis* (Wlk.)
June 20, 1991–July 31, 1989 Count 11
- 8364 *Phalaenostola larentioides* Grt.
July 22, 1988–July 24, 1989 Count 2
- 8368 *Tetanolia floridana* (Sm.)
June 3, 1992–July 31, 1989 Count 2
- 8370 *Bleptina caradrinalis* Gn.
June 20, 1991–July 31, 1989 Count 29
- 8378 *Renia salusalis* (Wlk.)
June 27, 1991–July 17, 1989 Count 15

- 8379 *Renia factiosalis* (Wlk.)
July 12, 1991–Aug. 21, 1992 Count 35
- 8381 *Renia discoloralis* Gn.
July 19, 1991–Aug. 27, 1992 Count 46
- 8386 *Renia adspersigillus* (Bosc)
June 26, 1992–Aug. 9, 1990 Count 27
- 8387 *Renia sobrialis* (Wlk.)
July 13, 1990–July 24, 1989 Count 10
- 8393 *Lascoria ambigualis* Wlk.
June 12, 1992–Aug. 21, 1989 Count 7
- 8397 *Palthis angulalis* (Hbn.)
May 30–Sep. 6, 1991 Count 30
- 8398 *Palthis asopialis* (Gn.)
May 30–Sep. 6, 1991 Count 9
- 8404 *Rivula propinquialis* Gn.
June 15–Sep. 24, 1988 Count 16
- 8412 *Melanomma auricinctaria* Grt.
May 30–Aug. 2, 1991 Count 4
- 8421 *Hypenodes fractilinea* (Sm.)
May 30, 1991–Aug. 3, 1990 Count 15
- 8426 *Dyspyralis illocata* Warr.
July 5, 1991–Aug. 19, 1988 Count 15
- 8427 *Dyspyralis puicticosta* (Sm.)
July 5, 1991–Aug. 7, 1989 Count 10
- 8428 *Dyspyralis nigella* (Stkr.)
July 19, 1991–Aug. 7, 1989 Count 8
- 8441 *Bomolocha manalis* (Wlk.)
June 19, 1989–Sep. 30, 1988 Count 11
- 8442 *Bomolocha baltimoralis* (Gn.)
May 12, 1988–Sep. 9, 1989 Count 81
- 8443 *Bomolocha bijugalis* (Wlk.)
May 21, 1989 Count 1
- 8444 *Bomolocha palparia* (Wlk.)
July 29, 1988 Count 1
- 8445 *Bomolocha abalienalis* (Wlk.)
June 15, 1988–Aug. 2, 1991 Count 4
- 8446 *Bomolocha deceptalis* (Wlk.)
May 30, 1991–Sep. 9, 1989 Count 29
- 8447 *Bomolocha madefactalis* (Gn.)
June 19, 1989–Aug. 30, 1991 Count 15
- 8448 *Bomolocha sordidula* (Grt.)
June 26, 1989–Aug. 2, 1991 Count 7
- 8465 *Plathypena scabra* (F.)
June 15, 1988–Nov. 21, 1992 Count 47
- 8479 *Spargaloma sexpunctata* Grt.
June 1–July 15, 1988 Count 10
- 8490 *Pangrapta decoralis* Hbn.
June 12, 1989–July 12, 1991 Count 2
- 8491 *Ledaea perditilis* (Wlk.)
July 17, 1992 Count 2
- 8499 *Metalectra discalis* (Grt.)
July 29, 1988 Count 1
- 8514 *Scolecocampa liburnia* (Gey.)
June 20, 1991–July 31, 1989 Count 30
- 8534 *Plusiodonta compressipalpis* Gn.
July 8, 1988–July 13, 1990 Count 3
- 8536 *Calyptra canadensis* (Bethune)
June 22–July 8, 1988 Count 3

8555	<i>Scoliopteryx libatrix</i> (L.) July 4, 1989	Count 1	8858	<i>Catocala crataegi</i> Saund. July 15, 1988–July 31, 1989	Count 3
8587	<i>Panopoda rufimargo</i> (Hbn.) June 20, 1991–Aug. 14, 1989	Count 67	8863	<i>Catocala mira</i> Grt. July 12, 1991–Aug. 9, 1990	Count 11
8588	<i>Panopoda carneicosta</i> Gn. June 20, 1991–Aug. 7, 1992	Count 10	8864	<i>Catocala grynea</i> (Cram.) July 8, 1988–Sep. 9, 1989	Count 27
8641	<i>Drasteria grandirena</i> (Haw.) July 4–July 10, 1989	Count 2	8867	<i>Catocala blandula</i> Hulst July 8, 1988–July 24, 1992	Count 2
8689	<i>Zale lunata</i> (Drury) July 8, 1988–Nov. 3, 1992	Count 2	8874	<i>Catocala minuta</i> Edw. Aug. 2, 1991	Count 1
8695	<i>Zale undularis</i> (Drury) June 26, 1989–July 8, 1988	Count 2	8878	<i>Catocala amica</i> (Hbn.) July 12, 1991–Aug. 7, 1992	Count 2
8697	<i>Zale minerea</i> (Gn.) May 12, 1988–June 29, 1990	Count 12	8878.1	<i>Catocala lineella</i> Grt. July 12, 1991–Aug. 24, 1990	Count 11
8700	<i>Zale squamularis</i> (Drury) May 12, 1988	Count 1	8887	<i>Trichophsia ni</i> (Hbn.) July 8, 1988	Count 1
8704+	<i>Zale helata</i> (Sm.) June 15–June 22, 1988	Count 2	8898	<i>Allagrapha aerea</i> (Hbn.) June 6, 1991–Aug. 24, 1990	Count 4
8716	<i>Zale unilineata</i> (Grt.) May 18–June 15, 1988	Count 6	8905	<i>Eosphoropteryx thyatyroides</i> (Gn.) July 31, 1989	Count 1
8717	<i>Zale horrida</i> Hbn. June 1, 1988–July 19, 1991	Count 5	8908	<i>Autographa precationis</i> (Gn.) May 18, 1988–Sep. 25, 1992	Count 9
8719	<i>Euparthenos nubilis</i> (Hbn.) June 19, 1989–Aug. 19, 1988	Count 24	8923	<i>Anagrapha ampla</i> (Wlk.) July 3, 1992	Count 1
8721	<i>Allotria elonympha</i> (Hbn.) June 12, 1989–Aug. 5, 1988	Count 16	8924	<i>Anagrapha falcifera</i> (Kby.) May 28, 1989–Sep. 10, 1988	Count 15
8727	<i>Parallelia bistriaris</i> Hbn. June 6, 1991–Sep. 9, 1989	Count 28	8955	<i>Marathyssa inficta</i> (Wlk.) June 15, 1990–July 31, 1989	Count 8
8738+	<i>Caenurgina crassiuscula</i> (Haw.) Aug. 4–Sep. 10, 1988	Count 18	8956	<i>Marathyssa basalis</i> Wlk. May 12, 1988	Count 1
8771	<i>Catocala piatrix</i> Grt. Sep. 7, 1990	Count 1	8957	<i>Paectes oculatrix</i> (Gn.) June 15–July 15, 1988	Count 13
8778	<i>Catocala habilis</i> Grt. Aug. 23, 1991–Oct. 10, 1992	Count 16	8969	<i>Baileya doubledayi</i> (Gn.) July 8, 1988	Count 1
8779	<i>Catocala serena</i> Edw. Aug. 3–Aug. 24, 1990	Count 6	8970	<i>Baileya ophthalmica</i> (Gn.) May 28, 1989–July 24, 1992	Count 26
8781	<i>Catocala judith</i> Stkr. July 24–Aug. 21, 1989	Count 5	8971	<i>Baileya dormitans</i> (Gn.) May 12, 1988–July 12, 1991	Count 74
8785	<i>Catocala residua</i> Grt. Aug. 7, 1989–Oct. 10, 1992	Count 12	8972	<i>Baileya levitans</i> (Sm.) May 4, 1988–Aug. 14, 1989	Count 77
8788	<i>Catocala relecta</i> Grt. Aug. 5, 1988–Sep. 14, 1990	Count 14	8973	<i>Baileya australis</i> (Grt.) June 12, 1989–Sep. 10, 1988	Count 12
8795	<i>Catocala palaeogama</i> Gn. July 12, 1991–Sep. 14, 1990	Count 15	8983	<i>Meganola minuscula</i> (Zell.) May 4, 1988–Aug. 7, 1989	Count 26
8797	<i>Catocala subnata</i> Grt. Aug. 27, 1992–Sep. 6, 1991	Count 2	8983.1	<i>Meganola phylla</i> (Dyar) May 28, 1992–Aug. 19, 1988	Count 5
8798	<i>Catocala neogama</i> (J.E. Smith) Sep. 14–Sep. 21, 1990	Count 2	8983.2	<i>Meganola spodia</i> Franc. June 8, 1990	Count 1
8801	<i>Catocala ilia</i> (Cram.) July 8–Sep. 10, 1988	Count 5	8990	<i>Nola cilicoides</i> (Grt.) June 6, 1991	Count 1
8802	<i>Catocala cerogama</i> Gn. Aug. 14, 1989–Sep. 30, 1988	Count 8	8992	<i>Nola triquetra</i> (Fitch) May 12, 1988	Count 1
8832	<i>Catocala cara</i> Gn. Oct. 10, 1992	Count 1	9037	<i>Hyperstrotia pervertens</i> (B. & McD.) June 6, 1991–July 29, 1988	Count 139
8846	<i>Catocala sordida</i> Grt. July 22, 1988–Sep. 4, 1992	Count 5	9038	<i>Hyperstrotia villificans</i> (B. & McD.) July 8, 1988	Count 2
8857	<i>Catocala ultronita</i> (Hbn.) July 12, 1991–Sep. 14, 1990	Count 30	9040	<i>Hyperstrotia secta</i> (Grt.) July 5, 1991–July 15, 1988	Count 14

- 9044 *Thioptera nigrofimbria* (Gn.)
July 19, 1991 Count 1
- 9047 *Lithacodia muscosula* (Gn.)
May 30–Aug. 16, 1991 Count 72
- 9048 *Lithacodia albidula* (Gn.)
June 20, 1991–Sep. 4, 1992 Count 14
- 9051 *Lithacodia musta* (G. & R.)
June 15–Aug. 5, 1988 Count 3
- 9053 *Pseudeustroia carneola* (Gn.)
May 30, 1991–Sep. 30, 1988 Count 135
- 9055.1 *Maliattha synochitis* (G. & R.)
May 30, 1991–Sep. 30, 1988 Count 48
- 9057 *Homophoberia apicosa* (Haw.)
June 20, 1991–Aug. 21, 1989 Count 6
- 9062 *Cerna ceriutha* (Tr.)
June 6, 1991–July 29, 1988 Count 18
- 9065 *Leuconycta diphetoides* (Gn.)
June 6, 1991–Aug. 14, 1989 Count 20
- 9066 *Leuconycta lepidula* (Grt.)
June 12, 1989–July 15, 1988 Count 2
- 9090 *Tarachidia candefacta* (Hbn.)
June 15–Aug. 19, 1988 Count 9
- 9095 *Tarachidia erastrioides* (Gn.)
May 30, 1991–Aug. 16, 1990 Count 15
- 9182 *Panthea furcilla* (Pack.)
June 6, 1991–Aug. 16, 1990 Count 17
- 9184 *Colocasia flavicornis* (Sm.)
July 22, 1988 Count 1
- 9185 *Colocasia propinqua* (Grt.)
May 12, 1988–June 26, 1992 Count 39
- 9189 *Charadra deridens* (Gn.)
May 12, 1988–June 29, 1990 Count 3
- 9193 *Raphia frater* Grt.
June 20–Aug. 2, 1991 Count 6
- 9200 *Acronicta americana* (Harr.)
June 27, 1991–July 15, 1988 Count 9
- 9203 *Acronicta dactylina* Grt.
July 24, 1992 Count 1
- 9227 *Acronicta laetifica* Sm.
Aug. 5, 1988–Aug. 16, 1991 Count 2
- 9229 *Acronicta hasta* Gn.
May 30, 1991–Aug. 26, 1988 Count 15
- 9235 *Acronicta spinigera* Gn.
May 30, 1991–July 29, 1988 Count 31
- 9236 *Acronicta morula* G. & R.
June 1–June 22, 1988 Count 3
- 9237 *Acronicta interrupta* Gn.
June 15, 1988 Count 1
- 9238 *Acronicta lobeliae* Gn.
May 12, 1988–July 31, 1989 Count 3
- 9243 *Acronicta ovata* Grt.
June 6, 1991–Aug. 5, 1988 Count 38
- 9244 *Acronicta modica* Wlk.
June 12, 1989–July 15, 1988 Count 19
- 9245+ *Acronicta haesiata* (Grt.)
May 30, 1991–Aug. 5, 1988 Count 234
- 9251 *Acronicta retardata* (Wlk.)
May 30, 1991–July 13, 1990 Count 8
- 9254 *Acronicta afflicta* Grt.
July 12, 1991 Count 1
- 9261 *Acronicta impressa* Wlk.
July 12, 1991–Aug. 7, 1989 Count 2
- 9285 *Polygrammate hebraeicum* Hbn.
May 30, 1991–Aug. 5, 1988 Count 35
- 9301 *Eudryas grata* (F.)
June 20, 1991–Aug. 5, 1988 Count 16
- 9328 *Apamea nigrior* (Sm.)
July 10, 1992 Count 1
- 9329 *Apamea cariosa* (Gn.)
July 19, 1991–Aug. 7, 1992 Count 5
- 9342 *Apamea multicolor* (Dyar)
July 10, 1992 Count 1
- 9348 *Apamea amputatrix* (Fitch)
July 13, 1990–July 31, 1989 Count 2
- 9362a *Apamea remissa indocilis* (Wlk.)
June 1, 1990 Count 3
- 9364 *Apamea sordens* (Hufn.)
June 1, 1990–June 26, 1992 Count 4
- 9367 *Apamea dubitans* (Wlk.)
July 24–Sep. 9, 1989 Count 7
- 9373 *Apamea helva* (Grt.)
Oct. 27, 1988 Count 1
- 9404 *Oligia modica* (Gn.)
Aug. 14, 1989–Sep. 10, 1988 Count 12
- 9406 *Oligia fractilinea* (Grt.)
July 19, 1991–Sep. 9, 1989 Count 15
- 9408 *Oligia exhausta* (Sm.)
July 12, 1991–July 15, 1988 Count 3
- 9419 *Oligia mactata* (Gn.)
Sep. 21, 1990–Oct. 16, 1988 Count 6
- 9427 *Meropieon diversicolor* (Morr.)
Sep. 7, 1990 Count 1
- 9452 *Macronoctua onusta* Grt.
Sep. 21, 1990–Sep. 30, 1988 Count 3
- 9454 *Amphipoea velata* (Wlk.)
July 5, 1991–July 24, 1989 Count 15
- 9457+ *Amphipoea americana* (Speyer)
July 15, 1988–July 31, 1992 Count 2
- 9466 *Papaipema cataphracta* (Grt.)
Sep. 30, 1988 Count 1
- 9473 *Papaipema impecuniosa* (Grt.)
Sep. 30, 1988–Oct. 10, 1992 Count 5
- 9483 *Papaipema inquaesita* (G. & R.)
Aug. 19, 1988–Oct. 10, 1992 Count 6
- 9485 *Papaipema baptisiae* (Bird)
Sep. 10–Sep. 24, 1988 Count 5
- 9505 *Papaipema cerussata* (Grt.)
Sep. 30, 1988 Count 1
- 9509 *Papaipema unimoda* (Sm.)
Sep. 9, 1989 Count 1
- 9520 *Achatodes zeae* (Harr.)
July 15, 1988 Count 1
- 9526 *Bellura densa* (Wlk.)
June 1, 1988 Count 1
- 9545 *Euplexia benesimilis* McD.
May 30, 1991–Aug. 26, 1988 Count 24

9546	<i>Phlogophora iris</i> Gn. June 22, 1988.....	Count 1
9547	<i>Phlogophora periculosa</i> Gn. Aug. 19, 1988–Sep. 13, 1991.....	Count 26
9555	<i>Ipinomorpha pleonectusa</i> Grt. July 12, 1991–Sep. 9, 1989.....	Count 7
9556	<i>Chytonix palliatricula</i> (Gn.) June 1, 1988–Aug. 7, 1989.....	Count 66
9578	<i>Hyppa xylinoides</i> (Gn.) May 12, 1988–Sep. 2, 1989.....	Count 15
9582	<i>Nedra ramosula</i> (Gn.) June 13–July 12, 1991.....	Count 2
9618	<i>Phosphila turbulenta</i> Hbn. July 12, 1991.....	Count 1
9619	<i>Phosphila miseloides</i> (Gn.) July 12–July 19, 1991.....	Count 2
9631	<i>Calloptistria mollissima</i> (Gn.) June 15, 1988–Aug. 9, 1990.....	Count 7
9638	<i>Amphipyra pyramidoides</i> Gn. July 31, 1989–Nov. 21, 1992.....	Count 161
9639	<i>Amphipyra tragopoginis</i> (Cl.) Aug. 31, 1990.....	Count 1
9647	<i>Athetis miranda</i> (Grt.) June 6, 1991–Aug. 19, 1988.....	Count 8
9650	<i>Anorthodes tarda</i> (Gn.) June 5, 1992–Sep. 10, 1988.....	Count 12
9662	<i>Balsa malana</i> (Fitch) June 19, 1989–Aug. 24, 1990.....	Count 7
9663	<i>Balsa tristrigella</i> (Wlk.) May 30, 1991–July 15, 1988.....	Count 49
9664	<i>Balsa labecula</i> (Grt.) May 30, 1991–Aug. 21, 1989.....	Count 15
9666	<i>Spodoptera frugiperda</i> (J.E. Smith) Sep. 13, 1991.....	Count 1
9669	<i>Spodoptera ornithogalli</i> (Gn.) Aug. 21, 1989–Oct. 16, 1988.....	Count 3
9678	<i>Elaphria versicolor</i> (Grt.) June 20, 1991–July 15, 1988.....	Count 9
9681	<i>Elaphria festivoides</i> (Gn.) May 30, 1991–July 3, 1992.....	Count 8
9688	<i>Galgula partita</i> Gn. June 1, 1988–Aug. 31, 1990.....	Count 20
9689	<i>Perigea xanthioides</i> Gn. June 15, 1988–Aug. 14, 1989.....	Count 6
9690	<i>Condica videns</i> (Gn.) June 27, 1991–Aug. 14, 1989.....	Count 2
9696	<i>Condica vecors</i> (Gn.) June 15, 1990–Aug. 5, 1988.....	Count 8
9720	<i>Ogdoconta cinereola</i> (Gn.) May 30, 1991–Aug. 21, 1989.....	Count 25
9815	<i>Cosmia calami</i> (Harv.) July 5, 1991–July 27, 1990.....	Count 23
9818	<i>Amolita fessa</i> Grt. June 20, 1991–July 15, 1988.....	Count 7
9874	<i>Xylena curvimaacula</i> (Morr.) Mar. 23, 1988.....	Count 1
9888	<i>Lithophane innominata</i> (Sm.) Mar. 23–May 12, 1988.....	Count 8
9892	<i>Lithophane disposita</i> Morr. Nov. 4, 1988.....	Count 1
9893	<i>Lithophane hemina</i> Grt. Mar. 23, 1988–Sep. 9, 1989.....	Count 3
9910	<i>Lithophane antennata</i> (Wlk.) Sep. 9, 1989.....	Count 1
9929	<i>Pyreferra hesperidago</i> (Gn.) May 2, 1988–May 21, 1989.....	Count 4
9933+	<i>Eupsilia vinulenta</i> (Grt.) Nov. 3, 1992–Nov. 4, 1988.....	Count 2
9936	<i>Eupsilia morrisoni</i> (Grt.) Nov. 4, 1988.....	Count 6
9946	<i>Epiglaea decliva</i> (Grt.) Nov. 21, 1992.....	Count 2
9957	<i>Stinira bicolorago</i> (Gn.) Sep. 9, 1989–Nov. 21, 1992.....	Count 82
9961	<i>Anathix ralla</i> (G. & R.) Aug. 7, 1989–Sep. 30, 1988.....	Count 30
10005	<i>Feralia jocosa</i> (Gn.) Mar. 23, 1988.....	Count 2
10014	<i>Psaphida rolandi</i> (Grt.) Mar. 23, 1988.....	Count 1
10021	<i>Copivaleria grotei</i> (Morr.) May 4, 1988.....	Count 1
10059	<i>Homohadena badistriga</i> (Grt.) July 10, 1989.....	Count 1
10067	<i>Adita chionanthi</i> (J.E. Smith) Aug. 31, 1990.....	Count 1
10200	<i>Cucullia asteroides</i> Gn. May 28, 1989.....	Count 1
10276	<i>Polia imbrifera</i> (Gn.) June 15–July 8, 1988.....	Count 2
10288+	<i>Polia detracta</i> (Wlk.) May 30–Aug. 30, 1991.....	Count 201
10292	<i>Melanchnra adjuncta</i> (Gn.) June 5–Sep. 4, 1992.....	Count 3
10299	<i>Lacanobia subjuncta</i> (G. & R.) June 15–July 8, 1988.....	Count 2
10397	<i>Lacinipolia renigera</i> (Steph.) June 1–Oct. 16, 1988.....	Count 69
10405	<i>Lacinipolia lorea</i> (Gn.) June 6, 1991–July 10, 1992.....	Count 31
10431	<i>Faronta diffusa</i> (Wlk.) July 19, 1991–Aug. 21, 1989.....	Count 2
10436	<i>Aletia oxygala</i> (Grt.) May 30, 1991–Sep. 10, 1988.....	Count 14
10438	<i>Pseudaletia unipuncta</i> (Haw.) May 4, 1988–Sep. 13, 1991.....	Count 70
10440	<i>Leucania litata</i> Gn. July 3, 1992.....	Count 1
10444+	<i>Leucania phragmatidicola</i> Gn. June 6, 1991–Sep. 2, 1989.....	Count 9
10446+	<i>Leucania multilinea</i> Wlk. May 30, 1991–Aug. 24, 1990.....	Count 14
10447	<i>Leucania commoides</i> Gn. July 3, 1992–Aug. 2, 1991.....	Count 6
10461+	<i>Leucania ursula</i> (Fbs.) May 30, 1991–Sep. 9, 1989.....	Count 99

10495+	<i>Orthosia hibisci</i> (Gn.) Mar. 23, 1988–May 21, 1989	Count 24
10501	<i>Crocigrapha normani</i> (Grt.) May 4, 1988–May 28, 1989	Count 7
10518	<i>Achatia distincta</i> Hbn. May 12, 1988	Count 1
10521	<i>Morrisonia confusa</i> (Hbn.) May 12, 1988–June 12, 1989	Count 38
10521.1	<i>Morrisonia latex</i> (Gn.) June 1–July 15, 1988	Count 20
10524	<i>Nephelodes minians</i> Gn. Aug. 26–Sep. 30, 1988	Count 48
10532	<i>Homorthodes furfurata</i> (Grt.) June 1, 1988–July 24, 1989	Count 39
10563	<i>Protorthodes oviduca</i> (Gn.) June 15, 1988	Count 1
10578	<i>Pseudorthodes vecors</i> (Gn.) May 30, 1991–Sep. 9, 1989	Count 55
10585	<i>Orthodes crenulata</i> (Butler) July 3–Sep. 4, 1992	Count 3
10587	<i>Orthodes cynica</i> Gn. May 12, 1988–July 17, 1989	Count 208
10627	<i>Tricholita signata</i> (Wlk.) Aug. 5–Sep. 30, 1988	Count 10
10663	<i>Agrotis ipsilon</i> (Hufn.) May 12, 1988–Aug. 25, 1992	Count 76
10674+	<i>Feltia subgothica</i> (Haw.) Aug. 14, 1989–Sep. 6, 1991	Count 10
10676	<i>Feltia herilis</i> (Grt.) July 22, 1988–Sep. 13, 1991	Count 26
10698.2	<i>Trichosilia geniculata</i> (G. & R.) Aug. 19, 1988–Sep. 9, 1989	Count 2
10793	<i>Euxoa scholastica</i> McD. July 10, 1989	Count 1
10812	<i>Euxoa bostoniensis</i> (Grt.) Mar. 23, 1988	Count 1
10891	<i>Ochropleura plecta</i> (L.) May 30, 1991–Sep. 25, 1992	Count 111
10903+	<i>Euagrotis illapsa</i> (Wlk.) June 22, 1988–Sep. 9, 1989	Count 5
10915	<i>Peridroma saucia</i> (Hbn.) June 22–Nov. 4, 1988	Count 4
10926	<i>Spaelotis clandestina</i> (Harr.) June 26, 1989	Count 1
10929	<i>Eurois occulta</i> (L.) July 29, 1988	Count 1
10942.1+	<i>Xestia dolosa</i> Franc. May 30, 1991–Oct. 23, 1992	Count 348
10943	<i>Xestia normaniana</i> (Grt.) Aug. 14, 1989–Sep. 14, 1990	Count 102
10944	<i>Xestia smithii</i> (Snell.) Aug. 21, 1989–Aug. 25, 1992	Count 36
10950+	<i>Xestia bicarnea</i> (Gn.) Aug. 16, 1990–Sep. 13, 1991	Count 85
10955	<i>Xestia badinodis</i> (Grt.) Sep. 13, 1991–Sep. 24, 1988	Count 3
10994	<i>Cerastis tenebrifera</i> (Wlk.) May 4, 1988–May 21, 1989	Count 5
11006	<i>Protolampra brunneicollis</i> (Grt.) June 22, 1990–Sep. 9, 1989	Count 10
11010	<i>Heptagrotis phyllophora</i> (Grt.) July 8, 1988–July 17, 1992	Count 2
11029+	<i>Abagrotis alternata</i> (Grt.) June 27, 1991–Oct. 10, 1992	Count 58
11063	<i>Pyrrhia</i> (near <i>umbra</i>) Sep. 9, 1989	Count 1
11068	<i>Helicoverpa zea</i> (Boddie) Sep. 9, 1989	Count 2
11135	<i>Schinia rivulosa</i> (Gn.) July 29, 1988	Count 1

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CHECKLIST OF THE MOTHS OF WALDEN II NATURE PRESERVE, LAKE COUNTY, OHIO (1988-1992) WITH ANALYSES OF ABUNDANCE

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ABSTRACT

The biodiversity of moths at Walden II Nature Preserve in Lake County, Ohio was studied by placing an ultraviolet light trap at the same location each year. The checklist tabulates five consecutive years of trapping (1988-1992) and includes 17,053 specimens representing 502 species. The study began in 1987 and continued through 1996, but only data for 1988-1992 are included here. The checklist is a historical record of the species that were present in 1988-1992 and the techniques used were designed so they can be duplicated in the future. The accumulation of species collected over time illustrates the importance of long-term studies. Species were still being added after ten years of trapping. The Shannon-Wiener Diversity Index for the moths collected in 1988-1992 is 7.1 and the Shannon-Wiener Evenness Index is 0.79. Two hundred twenty of the 502 species are widespread in northeast Ohio, having also been collected in Columbiana, Stark, and Ashland Counties. The less abundant species at Walden II are not less likely to be widespread than the more abundant species at Walden II, except for the singletons. One species of owl moth that was collected at Walden II is of special interest in Ohio. All specimens collected are deposited at The Cleveland Museum of Natural History, Cleveland, Ohio.

Introduction

The objective of this study was to document the population changes of native moths for ten years at several sites within the drainage basin of the Grand River in Trumbull, Ashtabula, and Lake Counties, Ohio, during gypsy moth invasion and control. This is the sixth in a series of checklists that tabulate the moths collected at each site during 1988–1992.

Over this same period, the population of the gypsy moth increased in the entire drainage basin. Pheromone trap catches of male gypsy moths increased at Walden II Nature Preserve from $43 \pm 7(3)$ per trap in 1987 [mean \pm standard error (number of traps)], to $71 \pm 13(4)$ in 1988, $158 \pm 40(4)$ in 1989, $72 \pm 21(4)$ in 1990, and $150 \pm 50(4)$ in 1991. Pheromone trapping was discontinued after 1991. Ultraviolet-light-trap catches of male gypsy moths also increased, from 1 in 1987, to 8 in 1988, 43 in 1989, 8 in 1990, 15 in 1991, and 49 in 1992, but noticeable defoliation was not observed at Walden II Nature Preserve.

The overall study provides baseline data on pre-outbreak moth diversity, as well as data on the impact of gypsy moth control agents.

Description of the Surveillance Site at Walden II Nature Preserve

Walden II Nature Preserve is composed of 49 ha of forest and is bordered by Blair Road on the south and the Grand River on the north (Figure 1). The Preserve is situated on the Euclid end moraine on 15–30 m of glacial drift, till, silt, and sand over bedrock (White, 1980, p. 5, Pl. 1).

The light trap at Walden II Nature Preserve was located in Leroy Township in Lake County on the bluff overlooking the Grand River at latitude $41^\circ 43' 26''$ N and longitude $81^\circ 08' 34''$ W (U.S. Geological Survey Painesville, Ohio, 7.5-minute quadrangle topographic map; Figure 1).

Walden II Nature Preserve is located approximately 17 km north/northeast of the National Oceanic and Atmospheric Administration weather station at Chardon. The station at Chardon measured an average temperature of 9° Celsius, an average annual precipitation of 120 cm, and an average annual snowfall of 220 cm for 1988–1992.

The composition of the canopy and understory was evaluated for the 2500 m² of forest centered on the surveillance trap (point-quarter technique, nine points;



Figure 1. Map of the study area (adapted from the U.S. Geological Survey Painesville, Ohio, 7.5-minute quadrangle topographic map). Shaded area delineates Walden II Nature Preserve; star indicates position of surveillance trap within the Preserve.

Table 1. Importance values for woody plants at the surveillance site at Walden II Nature Preserve. The inventory included all woody stems with a circumference of five or more cm. A stem was counted as canopy only if it reached the uppermost layer of vegetation. Author citations according to Kartesz (1994); common names according to Weishaupt (1971).

Woody Plant Species		Canopy	Understory
Maple, sugar	<i>Acer saccharum</i> Marsh.	143	104
Hemlock, eastern	<i>Tsuga canadensis</i> (L.) Carr.	59	57
Beech, American	<i>Fagus grandifolia</i> Ehrh.	53	84
Tuliptree	<i>Liriodendron tulipifera</i> L.	20	8
Elm, American	<i>Ulmus americana</i> L.	16	0
Oak, northern red	<i>Quercus rubra</i> L.	8	13
Ash	<i>Fraxinus</i> spp.	0	9
Alder, speckled	<i>Alnus incana</i> ssp. <i>rugosa</i> (Du Roi) Clausen	0	9
Cherry, black	<i>Prunus serotina</i> Ehrh.	0	8
Grape, summer	<i>Vitis aestivalis</i> Michx.	0	8

Cottam and Curtis, 1956; Cox, 1980). The area used for the evaluation, 0.25 ha, is smaller than the area from which the moths are drawn. The light was visible to human eyes at distances of 80–90 m at Walden. The importance values for the woody plants at the surveillance site at Walden II Nature Preserve are given in Table 1.

The herbaceous plants included: ill-scented trillium *Trillium erectum* L.; common trillium *Trillium grandiflorum* (Michx.) Salisb.; big bluestem *Andropogon gerardii* Vitman var. *gerardii*; and bluejoint *Calamagrostis canadensis* (Michx.) Beauv. (James K. Bissell, 1998, personal communication; author citations according to Kartesz, 1994). The surveillance trap was within 1000 m of a pond and within 1000 m of the floodplain of the Grand River. The species were selected from a larger list of Walden species on deposit in the Herbarium at The Cleveland Museum of Natural History.

Surveillance Techniques

One Ellisco®-type ultraviolet light trap (15 watt, BL) was operated at the same location each year, from late May through September. The light was controlled by a timer from 7 p.m. to 8 a.m., eastern daylight time. The trap was set up before 7 p.m. the evening of operation and emptied after 8 a.m. the next morning. Two killing agents, potassium cyanide and ethyl acetate, were used during each collecting period. Using both improved the condition of the moths in the catch as compared to using only one or the other. Collections were made one week apart regardless of weather. The entire catches were sorted and archived in cellophane envelopes and all data were computerized. All the specimens collected are deposited in the Insect Collection at The Cleveland Museum of Natural History.

Results and Discussion

A total of 17,053 specimens representing 502 species were collected in 1988–1992 (Appendix). Species were identified using Covell (1984), Ferguson (1985), Forbes (1923; 1948; 1954; 1960), Holland (1922), Rings et al. (1992), and Rockburne and Lafontaine (1976). Nomenclature for the Noctuidae was updated from that used by Hodes et al. (1983) to that used by Rings et al. (1992; after Poole, 1989). Crambidae is used according to Scholtens (1996). There are 34 species that have been designated as plus-groups (+). These are species that are easily confused with closely related species; the count for a plus group may therefore include individuals from more than one species.

The accumulation of species collected over time, from 1987 to 1996, is shown in Figure 2. In 1987 (not included in this checklist), 351 species were collected, and in 1996, after ten years, the total had reached 592 (1993–1996, also not included in this checklist). Figure 2 illustrates the importance of long-term studies. One or two years of monitoring would not have been long enough to estimate moth biodiversity at Walden II Nature Preserve and five years would have been a minimum. The species accumulation curve was still rising after ten years of sampling. Rings and Metzler (1989) estimated that 600 to 1000 moth species may be sampled in a locality with high host plant diversity if collections are made at frequent intervals over five or more years. Our data are consistent with that assertion. It is expected that the asymptote of the curve is well above 600 species since a number of categories of moths are missing from our checklist: fall, winter, and early spring moths are missing because collecting was not begun until the end of May and collecting ended in September. Some species of moths are poorly sampled by light trapping. Also, many Microlepidoptera that were collected are not included because of the difficulty of identifying them.

Our checklist is a historical record of the moth species that were present in 1988–1992. The techniques were designed so that they can be duplicated in the future to document the changes in moth diversity that follow changes in land use and weather.

Relative abundances of the 502 species are shown in Figure 3. The Shannon-Wiener Diversity function was used to measure species diversity (Krebs, 1994). This index takes into account both the number of species and the manner in which the individuals are distributed among the species. A greater number of species increases the index and a more even distribution of individuals among the species also increases the index. Evenness can vary from zero to one and an evenness of one indicates that all species have the same number of individuals. The Shannon-Wiener Diversity Index is 7.1 and the Shannon-Wiener Evenness Index is 0.79.

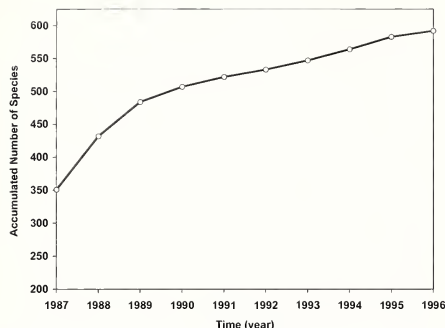


Figure 2. Plot of the annual accumulation of species collected at Walden II Nature Preserve, 1987–1996.

Almost six percent of the total count was composed of lesser maple spanworm moth *Itame pustularia* (6273) and sugar maple is the dominant canopy tree at this site. The next most abundant species was greater black-letter dart *Xestia dolosa* (10942.1+) whose larva feeds on apple, clover, maples, etc. Following, in order of decreasing abundance, were: banded tussock moth *Halysidota tessellaris* (8203+) whose larva feeds on many deciduous trees; rotund idia *Idia rotundalis* (8326) whose larva feeds on dead coral fungus and dead leaves; leafroller moth *Choristoneura fractivittana* (3632) whose larva feeds on

apple, beeches, birches, etc.; sod webworm *Crambus agitatellus* (5362+) whose larva feeds on grasses and low plants; forest tent caterpillar moth *Malacosoma disstria* (7698) whose larva feeds on trees and shrubs, especially aspens and maples; yellow-collared scape moth *Cispeps fulvicollis* (8267) whose larva feeds on grasses, lichens, and spike-rushes; cynical quaker *Orthodes cynica* (10587) whose larva feeds on plantain, dandelion, and developing goldenrod blossoms; and oecophorid *Antaeotricha leucilana* (1014+) whose larva feeds on many deciduous trees.

Figure 3 also indicates, with a vertical line, every species that had been collected at single locations in Columbiana County (Rings and Metzler, 1992), Stark County (Rings et al., 1987), and Ashland County (Rings and Metzler, 1989). A total of 220 Walden II species have been collected at all four sites and can be considered to be widespread in northeast Ohio. Data on a wide variety of plants and animals show a broad positive correlation between abundance and distribution (Gaston, 1988; 1990). Three explanations have been proposed (Krebs, 1994). First, the relationship is an artifact of sampling because rarer species are less likely to be found. Second, species that use a restricted variety of resources are less likely to be abundant and widespread. And third, species that disperse more are more common and widespread. Our data (Figure 3) suggest that a positive correlation between abundance and distribution does not exist, when abundance is viewed from the perspective of abundance at Walden II. Of the 220 Walden II species which are widespread in northeast Ohio, 89 had total counts of 10 or fewer at Walden II.

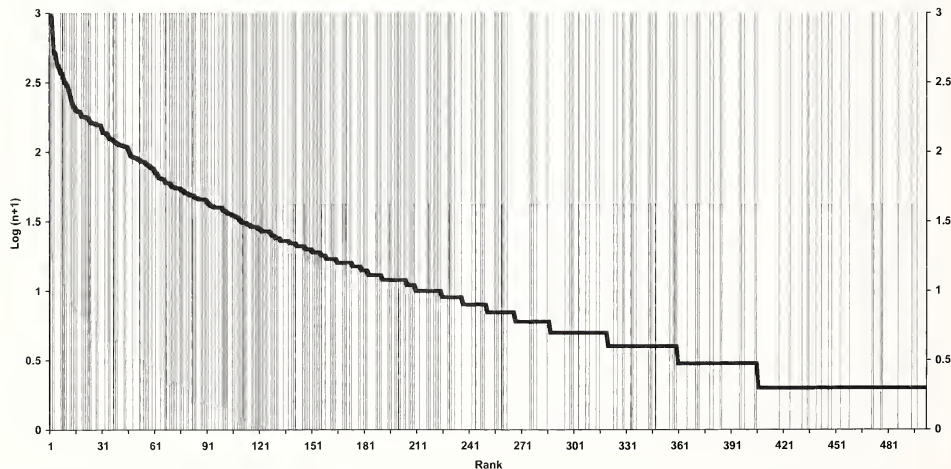


Figure 3. Plot of the logarithm of abundance versus rank. Vertical lines indicate species that are widespread in northeast Ohio. Species collected at Walden II Nature Preserve, 1988–1992.

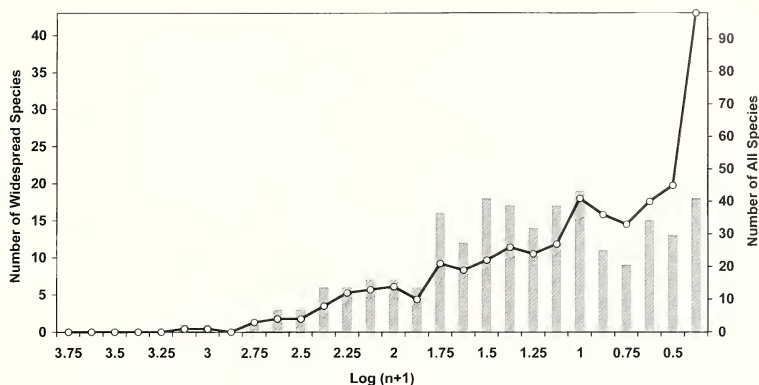


Figure 4. Correspondence between the total number of Walden II species in an abundance interval (line, scale at right) and the number of widespread Walden II species in the same abundance interval (bar, scale at left). Note that the y-axis scale for the widespread species is larger than the y-axis scale for the total number of species.

Overall, there is a close correspondence between the number of widespread species in an abundance interval and the total number of species (Figure 4). The exception is the decrease in the proportion of widespread species in the singleton interval. The 98 singleton species at Walden II include only 18 widespread species whereas the 45 doubleton species include 13 widespread species.

One species of owl moth collected at Walden II is listed as being of special interest in Rings et al. (1992): scurly quaker *Homorhodes furfurata* (10532) whose larva feeds on maples.

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Appendix. Checklist of species collected at Walden II Nature Preserve, 1988–92. Numbers preceding the species names are checklist numbers from Hodges et al. (1983). A plus-group (+) is a species that is easily confused with closely related species. Following the checklist number is the species name including author (abbreviations as listed in Hodges et al., 1983), date of collection, and count of specimens collected. When more than one collection date is listed, the first is the earliest seasonal date of collection and the second is the latest, both with the year in which that occurred. The count is the total number of specimens collected in 1988–1992.

Family TINEIDAE

- 372+ *Acrolophus plumifrontella* (Clem.)
June 22, 1988 Count 2

Family OECOPHORIDAE

- 881 *Agonopterix senicionella* (Bsk.)
July 29, 1988 Count 4
- 882 *Agonopterix robinella* (Pack.)
July 22–Sep. 10, 1988 Count 12
- 957 *Psilocorsis reflexella* Clem.
June 29, 1990–Aug. 30, 1991 Count 48
- 1014+ *Antaeotricha leucillana* (Zell.)
May 28, 1992–Aug. 31, 1990 Count 311
- 1046 *Callima argenticinctella* Clem.
July 10, 1989–Aug. 24, 1990 Count 7

Family GELECHIIDAE

- 2295 *Trichotaphe flavocostella* Clem.
Aug. 16, 1990 Count 1

Family YPONOMEUTIDAE

- 2401 *Atteva punctella* (Cram.)
June 8–Sep. 14, 1990 Count 42
- 2420 *Yponomenta multipunctella* Clem.
June 20, 1991–July 24, 1989 Count 111

Family Sesiidae

- 2554 *Synanthedon acerni* (Clem.)
June 19–July 31, 1989 Count 4

Family TORTRICIDAE

- 3361 *Ancylis semiovana* (Zell.)
June 15–Aug. 19, 1988 Count 75
- 3503 *Croesia semipurpurana* (Kft.)
June 15, 1988 Count 1
- 3594 *Pandemis limitata* (Rob.)
May 30, 1991–Sep. 14, 1990 Count 173
- 3623 *Argyrotaenia quercifoliola* (Fitch)
June 15, 1988–July 3, 1992 Count 9
- 3624 *Argyrotaenia alisellana* (Rob.)
June 6, 1991–June 26, 1992 Count 3
- 3625 *Argyrotaenia mariana* (Fern.)
June 4, 1989 Count 1
- 3632 *Choristoneura fractivittana* (Clem.)
May 30, 1991–Sep. 10, 1988 Count 425
- 3633 *Choristoneura parallela* (Rob.)
May 30, 1991–Sep. 4, 1992 Count 84
- 3635 *Choristoneura rosaceana* (Harr.)
May 30, 1991–Sep. 14, 1990 Count 155
- 3648 *Archips argyrospila* (Wlk.)
July 10, 1989 Count 3

- 3658 *Archips purpurana* (Clem.)
July 10, 1989 Count 2
- 3672 *Syndemis afflictana* (Wlk.)
May 18, 1988 Count 5
- 3686 *Clepsis melaleucana* (Wlk.)
May 30, 1991–June 26, 1992 Count 161
- 3720 *Sparganothis reticulatana* (Clem.)
July 10, 1989–Sep. 10, 1988 Count 15
- 3725 *Sparganothis petitana* (Rob.)
July 3–July 10, 1992 Count 4
- 3748 *Amorbia humerosana* Clem.
May 30, 1991–June 26, 1989 Count 20

Family ZYGAENIDAE

- 4624 *Harrisina americana* (Guer.)
June 22, 1990–July 17, 1992 Count 3

Family LIMACODIDAE

- 4652 *Tortricidia testacea* Pack.
May 30, 1991–July 4, 1989 Count 52
- 4654 *Tortricidia flexuosa* (Grt.)
May 30, 1991–Aug. 3, 1990 Count 136
- 4659 *Packardia geminata* (Pack.)
May 30, 1991–July 10, 1992 Count 19
- 4661 *Packardia elegans* (Pack.)
June 20, 1991–July 10, 1992 Count 2
- 4665 *Lithacodes fasciola* (H.-S.)
May 30–Aug. 30, 1991 Count 45
- 4667 *Apoda y-inversum* (Pack.)
June 20, 1991–July 17, 1992 Count 9
- 4669 *Apoda biguttata* (Pack.)
June 6, 1991–July 22, 1988 Count 7
- 4671 *Prolimacodes badia* (Hbn.)
June 26, 1989–Aug. 5, 1988 Count 9
- 4681 *Isa texnla* (H.-S.)
July 5, 1991–Aug. 5, 1988 Count 12
- 4685 *Adoneta spinuloides* (H.-S.)
June 27, 1991–July 29, 1988 Count 9
- 4697 *Euclea delphinii* (Bdv.)
May 30–Aug. 23, 1991 Count 34
- 4700 *Sibine stimulea* (Clem.)
July 22, 1988 Count 1

Family CRAMBIDAE

- 4703 *Gesneria centuriella* (D. & S.)
June 12–Aug. 21, 1989 Count 194
- 4748 *Munroessa iccinialis* (Wlk.)
Aug. 23, 1991 Count 1
- 4751 *Munroessa gyralis* (Hulst)
June 20, 1991–Sep. 9, 1989 Count 2

4761	<i>Parapoynx badiusalis</i> (Wlk.) Aug. 14, 1989.....	Count 1
4774	<i>Petrophila bifascialis</i> (Rob.) Sep. 9, 1989.....	Count 1
4889	<i>Dicymolomia julianalis</i> (Wlk.) June 22, 1988–Sep. 7, 1990.....	Count 4
4897	<i>Evergestis pallidata</i> (Hufn.) June 15, 1988–Sep. 7, 1990.....	Count 5
4936	<i>Saurobotrys fuitalis</i> (Led.) June 5–July 3, 1992.....	Count 5
4937	<i>Nascia acutella</i> (Wlk.) May 30–Aug. 2, 1991.....	Count 8
4944	<i>Crocidophora serratissimalis</i> Zell. June 20, 1991–Sep. 2, 1989.....	Count 8
4945	<i>Crocidophora tubercularis</i> Led. May 30, 1991–July 24, 1989.....	Count 11
4949	<i>Ostrinia nubilalis</i> (Hbn.) May 30–Aug. 30, 1991.....	Count 55
4953a	<i>Phlyctaenia coronata tertialis</i> (Gn.) May 30–Aug. 30, 1991.....	Count 13
4962	<i>Hahncappsa marculenta</i> (G. & R.) June 15, 1988–Sep. 9, 1989.....	Count 9
4980	<i>Helviborys helvialis</i> (Wlk.) July 8, 1988.....	Count 8
4991	<i>Sericoplaga externalis</i> Warr. Aug. 14, 1989.....	Count 1
5040	<i>Pyrausta bicoloralis</i> (Gn.) May 30, 1991–Sep. 9, 1989.....	Count 14
5071	<i>Pyrausta acronialis</i> (Wlk.) June 20, 1991–Sep. 7, 1990.....	Count 4
5079	<i>Udea rubigalis</i> (Gn.) May 30, 1991–Sep. 14, 1990.....	Count 90
5142	<i>Diacme elealis</i> (Wlk.) June 29–July 27, 1990.....	Count 15
5156	<i>Nomophila nearctica</i> Mun. July 12–Aug. 16, 1991.....	Count 2
5159	<i>Desmia fimeralis</i> (Hbn.) May 30, 1991–Sep. 10, 1988.....	Count 179
5182	<i>Blepharomastix ranalis</i> (Gn.) June 22–July 27, 1990.....	Count 39
5226	<i>Palpiia magniferalis</i> (Wlk.) May 30–Aug. 23, 1991.....	Count 100
5228	<i>Polygrammodes flavidalis</i> (Gn.) July 4, 1989–Aug. 24, 1990.....	Count 2
5241	<i>Pantographa limata</i> (G. & R.) June 27, 1991–Sep. 4, 1992.....	Count 84
5272	<i>Herpetogramma bipunctalis</i> (F.) June 12–Sep. 9, 1989.....	Count 29
5275	<i>Herpetogramma pertextalis</i> (Led.) June 12–Aug. 21, 1989.....	Count 39
5277	<i>Herpetogramma thestalis</i> (Wlk.) July 3, 1992.....	Count 11
5280	<i>Herpetogramma aeglealis</i> (Wlk.) July 10, 1992–Aug. 2, 1991.....	Count 20
5362+	<i>Crambus agitatellus</i> Clem. June 5, 1992–Sep. 2, 1989.....	Count 407
5392	<i>Aegipia turbatella</i> Wlk. July 17, 1992.....	Count 1

5403	<i>Agriphila vulgigagella</i> (Clem.) Sep. 10, 1992.....	Count 1
5464	<i>Urola nivalis</i> (Drury) July 10, 1989–July 15, 1988.....	Count 4

Family PYRALIDAE

5518	<i>Aglossa cuprina</i> Zell. June 6, 1991–Aug. 27, 1992.....	Count 88
5524	<i>Hypsopygia costalis</i> (F.) June 15, 1988–Sep. 9, 1989.....	Count 176
5532	<i>Herculia infimbrialis</i> Dyar July 8, 1988–Aug. 21, 1989.....	Count 12
5533	<i>Herculia olinalis</i> (Gn.) July 13, 1990–Aug. 5, 1988.....	Count 3
5552	<i>Galasa nigrinodis</i> (Zell.) July 5, 1991.....	Count 1
5556	<i>Tosale oviplagalis</i> (Wlk.) June 26, 1989–Aug. 7, 1992.....	Count 50
5571	<i>Condylolomia participalis</i> Grt. June 20, 1991–Aug. 14, 1989.....	Count 155
5577	<i>Epipaschia superatalis</i> Clem. June 22, 1988–July 27, 1990.....	Count 7
5606	<i>Tetralopha asperatella</i> (Clem.) June 29, 1990.....	Count 1
5997	<i>Euzophera ostricorella</i> Hulst June 15, 1988–July 20, 1990.....	Count 9
6053	<i>Peoria approximella</i> (Wlk.) June 22, 1990–July 24, 1989.....	Count 3

Family THYRIDIDAE

6079	<i>Dysodia granulata</i> (Neum.) July 17–Sep. 9, 1989.....	Count 5
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Family THYATIRIDAE

6237	<i>Pseudothyatira cymatophoroides</i> (Gn.) Aug. 14, 1989.....	Count 1
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Family DREPANIDAE

6251	<i>Drepana arcuata</i> Wlk. June 5, 1992–Aug. 24, 1990.....	Count 10
6255	<i>Oreta rosea</i> (Wlk.) May 30, 1991–Sep. 24, 1988.....	Count 3

Family GEOMETRIDAE

6261	<i>Heliomatia cycladata</i> G. & R. May 30, 1991–July 3, 1992.....	Count 37
6270	<i>Protitame virginialis</i> (Hulst) June 26, 1989–Aug. 24, 1990.....	Count 7
6273	<i>Itame pustularia</i> (Gn.) June 20, 1991–Sep. 4, 1992.....	Count 1004
6299	<i>Itame coartaria</i> (Hulst) June 20, 1991–July 10, 1989.....	Count 3
6303	<i>Itame subcessaria</i> (Wlk.) July 17, 1992–July 24, 1989.....	Count 2
6335+	<i>Semiothisa aequiferaria</i> (Wlk.) June 1, 1990–Sep. 9, 1989.....	Count 40
6340	<i>Semiothisa minorata</i> (Pack.) July 12, 1991–Aug. 16, 1990.....	Count 4
6342	<i>Semiothisa bisignata</i> (Wlk.) June 22, 1988–Aug. 16, 1991.....	Count 3

6344+	<i>Semiothisa signaria</i> (Hbn.) May 30–Sep. 13, 1991	Count 198	6763	<i>Nacophora quernaria</i> (J.E. Smith) June 8, 1988	Count 1
6360	<i>Semiothisa quadrimotaria</i> (H.-S.) June 12, 1992–July 31, 1989	Count 5	6796	<i>Campaea perlata</i> (Gn.) May 30, 1991–Sep. 21, 1990	Count 110
6386	<i>Semiothisa ocellinata</i> (Gn.) June 15, 1988–Sep. 9, 1989	Count 78	6797	<i>Emmotos magnaria</i> Gn. July 31, 1989–Aug. 24, 1990	Count 2
6405	<i>Semiothisa gnophosaria</i> (Gn.) July 5, 1991–Aug. 24, 1990	Count 4	6798	<i>Emmotos subsignaria</i> (Hbn.) June 20, 1991–Sep. 4, 1992	Count 294
6486	<i>Turnos scolopacinaris</i> (Gn.) June 15, 1988	Count 1	6819	<i>Metanema inatomaria</i> Gn. June 15–Aug. 3, 1990	Count 6
6583	<i>Anacamptodes ephyraria</i> (Wlk.) June 20, 1991–Aug. 14, 1989	Count 16	6823	<i>Metarranthis angularia</i> B. & McD. July 4, 1989	Count 1
6584	<i>Anacamptodes lumaria</i> (Gn.) June 27–July 12, 1991	Count 2	6825	<i>Metarranthis indeclinata</i> (Wlk.) May 30, 1991–June 5, 1992	Count 4
6586	<i>Anacamptodes defectaria</i> (Gn.) July 13, 1990	Count 1	6826	<i>Metarranthis hypocharia</i> (H.-S.) May 30, 1991–July 3, 1992	Count 22
6588	<i>Iridopsis larvaria</i> (Gn.) May 30, 1991–Sep. 7, 1990	Count 31	6835	<i>Cepphis armataria</i> (H.-S.) June 20, 1991–July 13, 1990	Count 5
6590	<i>Anavitrinella pampinaria</i> (Gn.) May 28, 1989–Sep. 10, 1988	Count 17	6836	<i>Anagoga occiduararia</i> (Wlk.) July 29, 1988–Aug. 14, 1989	Count 18
6597	<i>Ectropis crepuscularia</i> (D. & S.) June 20–Sep. 13, 1991	Count 48	6838+	<i>Probole amicaria</i> (H.-S.) May 30, 1991–July 17, 1992	Count 54
6598	<i>Protocharmia porcelaria</i> (Gn.) July 24, 1989–Aug. 5, 1988	Count 2	6840	<i>Plagodis serinaria</i> H.-S. May 28, 1989–July 3, 1992	Count 159
6599	<i>Epinecis hortaria</i> (F.) May 21–Aug. 14, 1989	Count 44	6841	<i>Plagodis kuetzingi</i> (Grt.) June 15, 1988	Count 2
6620+	<i>Melanophia canadaria</i> (Gn.) May 21, 1989–Sep. 6, 1991	Count 50	6842	<i>Plagodis phlogosaria</i> (Gn.) July 10, 1989–July 27, 1990	Count 4
6638	<i>Enfidonia notataria</i> (Wlk.) June 1, 1990–June 15, 1988	Count 32	6844	<i>Plagodis alcoalaria</i> (Gn.) June 1, 1990–July 31, 1989	Count 30
6640a	<i>Biston betularia cognataria</i> (Gn.) June 8, 1988–July 24, 1989	Count 3	6863	<i>Caripeta divisata</i> Wlk. July 24, 1989–Aug. 19, 1988	Count 7
6654	<i>Hypagyrtis unipunctata</i> (Haw.) June 15, 1988–Sep. 2, 1989	Count 8	6884	<i>Besma endropiaria</i> (G. & R.) May 30, 1991–July 15, 1988	Count 64
6655	<i>Hypagyrtis esther</i> (Barnes) May 30, 1991–Sep. 7, 1990	Count 108	6885	<i>Besma quercivoraria</i> (Gn.) June 19, 1989–Aug. 27, 1992	Count 10
6667	<i>Lomographa vestaliata</i> (Gn.) May 30, 1991–July 10, 1992	Count 30	6888	<i>Lambdina fiscellaria</i> (Gn.) Sep. 21, 1990–Sep. 25, 1992	Count 5
6677	<i>Cabera erythemaria</i> Gn. June 4, 1989–Aug. 21, 1992	Count 17	6906	<i>Nepytia canosaria</i> (Wlk.) Sep. 24, 1988	Count 5
6678	<i>Cabera variolaria</i> Gn. June 8, 1990–Aug. 14, 1989	Count 2	6912	<i>Sicya macularia</i> (Harr.) June 20, 1991–July 8, 1988	Count 11
6680	<i>Cabera quadrifasciaria</i> (Pack.) June 22, 1988	Count 1	6941	<i>Eusarca confusaria</i> Hbn. July 4–Sep. 2, 1989	Count 11
6720	<i>Lyttosia unitaria</i> (H.-S.) June 20, 1991–July 10, 1992	Count 22	6963	<i>Tetracis crocallata</i> Gn. June 6, 1991–July 17, 1992	Count 4
6724	<i>Euchlaena serrata</i> (Drury) July 8, 1988	Count 1	6964	<i>Tetracis cachexiata</i> Gn. May 30, 1991–June 26, 1992	Count 87
6725	<i>Euchlaena muzaria</i> (Wlk.) June 15, 1988–July 10, 1992	Count 6	6965	<i>Engonobapta nivosaria</i> (Gn.) June 20, 1991–Sep. 9, 1989	Count 35
6729	<i>Euchlaena johnsonaria</i> (Fitch) June 12, 1989–Aug. 24, 1990	Count 3	6966	<i>Entrepala clemataria</i> (J.E. Smith) May 21, 1989–Aug. 23, 1991	Count 46
6739	<i>Euchlaena irriaria</i> (B. & McD.) June 26, 1992	Count 1	6982	<i>Prochoerodes transversata</i> (Drury) June 20, 1991–Sep. 24, 1988	Count 55
6740+	<i>Xanthotype urticaria</i> Swett May 30, 1991–Aug. 14, 1989	Count 4	6987	<i>Antepione thisoaria</i> (Gn.) July 12, 1991–Aug. 5, 1988	Count 7
6753+	<i>Pero honestaria</i> (Wlk.) May 21, 1989–Aug. 27, 1992	Count 117	6989	<i>Antepione indiscretata</i> (Hy. Edw.) July 15, 1988	Count 1

7009	<i>Nematocampa limbata</i> (Haw.) June 26, 1989–July 31, 1992.....	Count 15
7046+	<i>Nemoria bistriaria</i> Hbn. July 15, 1988–Aug. 27, 1992.....	Count 15
7048	<i>Nemoria mimosaria</i> (Gn.) May 30, 1991–June 5, 1992.....	Count 3
7053	<i>Dichorda iridaria</i> (Gn.) July 12, 1991–Aug. 5, 1988.....	Count 2
7058	<i>Synchlora aerata</i> (F.) May 30–Aug. 30, 1991.....	Count 2
7071	<i>Chlorochlamys chloroleucaria</i> (Gn.) Aug. 30, 1991.....	Count 1
7132	<i>Pleuroprucha insulsaria</i> (Gn.) May 30, 1991–Sep. 21, 1990.....	Count 63
7139	<i>Cyclophora pendulinaria</i> (Gn.) Aug. 2, 1991.....	Count 1
7146	<i>Haematopsis grataria</i> (F.) Aug. 14–Sep. 9, 1989.....	Count 3
7159	<i>Scopula limboundata</i> (Haw.) June 19, 1989–Sep. 10, 1988.....	Count 59
7169	<i>Scopula inductata</i> (Gn.) July 20, 1990.....	Count 1
7189	<i>Dysstroma hersiliata</i> (Gn.) June 27, 1991–July 3, 1992.....	Count 2
7196+	<i>Eulithis diversilineata</i> (Hbn.) July 5, 1991–Sep. 25, 1992.....	Count 27
7206	<i>Eulithis explanata</i> (Wlk.) July 27, 1990.....	Count 1
7290	<i>Coryphista meadii</i> (Pack.) July 19, 1991.....	Count 2
7307	<i>Mesoleuca ruficollata</i> (Gn.) June 15, 1988.....	Count 1
7330	<i>Anticlea multiflerata</i> (Wlk.) June 12, 1992.....	Count 1
7368	<i>Xanthorhoe labradorensis</i> (Pack.) May 18–Sep. 24, 1988.....	Count 16
7371	<i>Xanthorhoe idnata</i> (Gn.) June 12, 1989.....	Count 1
7388	<i>Xanthorhoe ferrugata</i> (Cl.) May 30, 1991–June 12, 1989.....	Count 3
7390	<i>Xanthorhoe lacustrata</i> (Gn.) May 30, 1991–Sep. 9, 1989.....	Count 34
7394	<i>Epirrhoe alternata</i> (Muller) June 19–Aug. 21, 1989.....	Count 2
7399a	<i>Euphyia unangulata intermedia</i> (Gn.) May 30, 1991–Sep. 10, 1988.....	Count 8
7414	<i>Orthonama obsipata</i> (F.) May 28–Sep. 9, 1989.....	Count 22
7416	<i>Orthonama centrostrigaria</i> (Woll.) May 30, 1991–Sep. 9, 1989.....	Count 92
7422	<i>Hydrelia inornata</i> (Hulst) May 30, 1991–Aug. 16, 1990.....	Count 7
7430	<i>Trichodezia albivittata</i> (Gn.) July 19, 1991–Aug. 27, 1992.....	Count 3
7440	<i>Eubaphe mendica</i> (Wlk.) June 22, 1990.....	Count 1
7445	<i>Horisme intestinata</i> (Gn.) June 22, 1988–Sep. 9, 1989.....	Count 6

7474+	<i>Eupithecia miserulata</i> Grt. May 28–Sep. 25, 1992.....	Count 196
7647	<i>Heterophleps triguttaria</i> H.-S. July 8, 1988.....	Count 1
7648	<i>Dyspteris abortivaria</i> (H.-S.) May 30, 1991–Aug. 14, 1989.....	Count 12

Family MIMALLONIDAE

7659	<i>Lacosoma chiridota</i> Grt. June 15, 1988.....	Count 1
7662	<i>Cicinnus melsheimeri</i> (Harr.) June 15–June 29, 1988.....	Count 2

Family APATELODIDAE

7663	<i>Apateles torrefacta</i> (J.E. Smith) June 20, 1991–June 29, 1990.....	Count 3
7665	<i>Olceclostera angelica</i> (Grt.) July 4, 1989–July 22, 1988.....	Count 5

Family LASIOCAMPIDAE

7670	<i>Tolype velleda</i> (Stoll) July 27, 1990–Sep. 25, 1992.....	Count 24
7673	<i>Tolype laricis</i> (Fitch) July 5, 1991–Sep. 10, 1988.....	Count 54
7675	<i>Tolype minuta</i> Dyar July 29, 1988.....	Count 1
7698	<i>Malacosoma dissidia</i> Hbn. June 20, 1991–July 31, 1989.....	Count 371
7701	<i>Malacosoma americanum</i> (F.) June 15, 1988–July 17, 1989.....	Count 84

Family SATURNIIDAE

7715	<i>Dryocampa rubicunda</i> (F.) May 30, 1991–July 24, 1989.....	Count 45
7723	<i>Anisota virginiana</i> (Drury) May 30, 1991.....	Count 1
7746	<i>Automeris io</i> (F.) June 4–July 4, 1989.....	Count 7
7758	<i>Actias luna</i> (L.) June 15, 1990–July 8, 1988.....	Count 2
7765	<i>Callosamia angulifera</i> (Wlk.) June 15, 1988–July 27, 1990.....	Count 7

Family SPHINGIDAE

7787	<i>Ceratomia undulosa</i> (Wlk.) May 28, 1992.....	Count 1
7824	<i>Paonias excaecatus</i> (J.E. Smith) June 13, 1991–July 31, 1989.....	Count 5
7825	<i>Paonias myops</i> (J.E. Smith) May 28, 1992–Aug. 16, 1990.....	Count 9
7827	<i>Loathoe juglandis</i> (J.E. Smith) May 30, 1991–July 17, 1989.....	Count 6
7828	<i>Pachysphinx modesta</i> (Harr.) June 4, 1989.....	Count 1
7870	<i>Sphecodina abbottii</i> (Swainson) June 15, 1988.....	Count 1
7871	<i>Deidamia inscripta</i> (Harr.) May 14–June 19, 1989.....	Count 12
7885	<i>Darapsa myron</i> (Cram.) June 19, 1989–July 29, 1988.....	Count 4

Family NOTODONTIDAE

7895	<i>Clostera albosigma</i> Fitch June 6, 1991–Aug. 7, 1992	Count 4
7898	<i>Clostera strigosa</i> (Grt.) July 12, 1991–July 29, 1988	Count 3
7901	<i>Clostera apicalis</i> (Wlk.) May 21, 1989–Aug. 9, 1990	Count 9
7902	<i>Datana ministra</i> (Drury) June 22, 1990	Count 1
7906+	<i>Datana contracta</i> Wlk. June 27, 1991–July 27, 1990	Count 9
7915	<i>Nadata gibbosa</i> (J.E. Smith) May 30, 1991–Aug. 21, 1992	Count 76
7917	<i>Hyperaeschra georgica</i> (H.-S.) June 4–June 19, 1989	Count 5
7919	<i>Peridea basitriens</i> (Wlk.) May 30, 1991–Aug. 21, 1989	Count 179
7920	<i>Peridea angulosa</i> (J.E. Smith) May 30, 1991–Aug. 26, 1988	Count 26
7921	<i>Peridea ferruginea</i> (Pack.) July 10, 1989	Count 1
7922	<i>Pheosia rimosa</i> Pack. June 29, 1988–Aug. 3, 1990	Count 3
7924	<i>Odontotia elegans</i> (Stkr.) June 26, 1989–Aug. 19, 1988	Count 2
7929	<i>Nerice bidentata</i> Wlk. June 19, 1989–Aug. 26, 1988	Count 10
7930	<i>Elidia caniplaga</i> (Wlk.) June 1, 1990–July 24, 1989	Count 23
7931	<i>Glaphisia septentrionis</i> Wlk. June 15, 1988–Aug. 9, 1990	Count 8
7936	<i>Furcula borealis</i> (Guer.-Meneville) July 22, 1988–Aug. 9, 1990	Count 6
7939	<i>Furcula occidentalis</i> (Lint.) July 17, 1989	Count 1
7951+	<i>Synnerista albifrons</i> (J.E. Smith) May 30, 1991–Aug. 21, 1992	Count 63
7957	<i>Dasylophia anguina</i> (J.E. Smith) Aug. 16, 1990	Count 1
7958	<i>Dasylophia thyatiroides</i> (Wlk.) June 15, 1988–July 31, 1989	Count 2
7974	<i>Misogada unicolor</i> (Pack.) May 30, 1991–July 24, 1989	Count 4
7975	<i>Macrurocampa marthesia</i> (Cram.) July 4, 1989–Aug. 9, 1990	Count 26
7994	<i>Heterocampa guttivitta</i> (Wlk.) May 30, 1991–Aug. 9, 1990	Count 156
7995	<i>Heterocampa biundata</i> Wlk. July 26, 1991–Aug. 21, 1989	Count 5
7998	<i>Lochmaeus nanteo</i> Doubleday July 22, 1988	Count 1
7999	<i>Lochmaeus bilineata</i> (Pack.) June 1–Aug. 16, 1990	Count 24
8005	<i>Schizura ipomoeae</i> Doubleday June 22–Aug. 5, 1988	Count 6
8006	<i>Schizura badia</i> (Pack.) July 3, 1992–Aug. 9, 1990	Count 4
8007	<i>Schizura unicornis</i> (J.E. Smith) May 30, 1991–Aug. 16, 1990	Count 23

8011	<i>Schizura leptinoides</i> (Grt.) May 30, 1991–Aug. 19, 1988	Count 15
8012	<i>Oligocentria semirufescens</i> (Wlk.) June 15, 1988	Count 2
8017	<i>Oligocentria lignicolor</i> (Wlk.) June 15, 1988–Aug. 7, 1992	Count 5

Family ARCTIIDAE

8045.1	<i>Crambidia pallida</i> Pack. July 13, 1990	Count 1
8107	<i>Haploa clymene</i> (Brown) July 12, 1991–July 31, 1989	Count 14
8121+	<i>Holomelina aurantiaca</i> (Hbn.) June 20, 1991–Aug. 16, 1990	Count 111
8129	<i>Pyrharctia isabella</i> (J.E. Smith) June 6, 1991–Sep. 10, 1992	Count 48
8133	<i>Spilosoma latipennis</i> Stretch May 30, 1991–July 6, 1990	Count 33
8134	<i>Spilosoma congrua</i> Wlk. May 21, 1989–July 17, 1992	Count 178
8137	<i>Spilosoma virginica</i> (F.) June 12, 1989–Aug. 19, 1988	Count 26
8140	<i>Hyphantria cunea</i> (Drury) May 30, 1991–Aug. 16, 1990	Count 15
8156	<i>Phragmatobia fuliginosa</i> (L.) July 15–Aug. 5, 1988	Count 3
8169+	<i>Apantesis phalerata</i> (Harr.) June 19, 1989–Aug. 27, 1992	Count 11
8197	<i>Apantesis virgo</i> (L.) July 31, 1989	Count 1
8203+	<i>Halysidota tessellaris</i> (J.E. Smith) May 30–Sep. 13, 1991	Count 525
8211	<i>Lophocampa caryae</i> Harr. May 30, 1991–June 15, 1988	Count 11
8230	<i>Cynia tenera</i> Hbn. June 22, 1988–Aug. 3, 1990	Count 6
8231	<i>Cynia oregonensis</i> (Stretch) June 5, 1992–July 29, 1988	Count 9
8238	<i>Enchaetes egle</i> (Drury) June 20, 1991–July 24, 1989	Count 7
8262	<i>Ctenucha virginica</i> (Esp.) June 20, 1991–June 22, 1988	Count 2
8267	<i>Cisseps fulvicollis</i> (Hbn.) May 28, 1992–Sep. 21, 1990	Count 363

Family LYMANTRIIDAE

8304	<i>Dasychira plagiata</i> (Wlk.) July 17, 1992–July 24, 1989	Count 2
8314	<i>Orgyia defuncta</i> Pack. Sep. 6, 1991–Sep. 24, 1988	Count 8
8316	<i>Orgyia leucostigma</i> (J.E. Smith) Aug. 30, 1991–Sep. 21, 1990	Count 3
8318	<i>Lynantria dispar</i> (L.) June 27, 1991–Aug. 27, 1992	Count 123

Family NOCTUIDAE

8322	<i>Idia americalis</i> (Gn.) June 15, 1988–Sep. 25, 1992	Count 54
8323+	<i>Idia aemula</i> Hbn. May 30, 1991–Sep. 25, 1992	Count 217

- 8326 *Idia rotundalis* (Wlk.)
July 5, 1991–Aug. 31, 1990 Count 507
- 8327 *Idia forbesi* (French)
July 10, 1989–Aug. 27, 1992 Count 137
- 8328 *Idia julia* (B. & McD.)
July 17, 1989 Count 1
- 8329 *Idia diminutis* (B. & McD.)
July 5, 1991–Aug. 21, 1989 Count 113
- 8330 *Idia scobialis* (Grt.)
July 13, 1990–July 17, 1989 Count 5
- 8334 *Idia lubricalis* (Gey.)
June 26, 1989–Aug. 23, 1991 Count 18
- 8338 *Phalaenophana pyramusalis* (Wlk.)
June 5–Aug. 21, 1992 Count 4
- 8340 *Zanclognatha litralis* (Hbn.)
June 5, 1992–Aug. 5, 1988 Count 41
- 8345 *Zanclognatha laevigata* (Grt.)
July 4, 1989–Aug. 27, 1992 Count 59
- 8348 *Zanclognatha pedipilalis* (Gn.)
June 15, 1990–Aug. 21, 1989 Count 4
- 8351 *Zanclognatha cruralis* (Gn.)
June 19, 1989–July 8, 1988 Count 6
- 8352+ *Zanclognatha jacchusalis* (Wlk.)
June 29, 1990–Sep. 25, 1992 Count 161
- 8355 *Chytolita morbidalis* (Gn.)
May 30, 1991–July 8, 1988 Count 39
- 8356 *Chytolita petrealis* Grt.
July 3, 1992 Count 1
- 8358 *Macrochilo litophora* (Grt.)
July 5, 1991–July 24, 1989 Count 4
- 8362 *Phalaenostola metonalis* (Wlk.)
June 12, 1992–July 8, 1988 Count 4
- 8363 *Phalaenostola eumehsalis* (Wlk.)
July 31, 1989 Count 1
- 8368 *Tetanolita floridana* (Sm.)
July 10, 1992 Count 1
- 8370 *Bleptina caradrinalis* Gn.
June 22, 1988–Sep. 9, 1989 Count 39
- 8378 *Renia salusalis* (Wlk.)
June 22–Aug. 19, 1988 Count 22
- 8379 *Renia factiosalis* (Wlk.)
July 17, 1989–Aug. 26, 1988 Count 93
- 8381 *Renia discoloralis* Gn.
July 12, 1991–Sep. 10, 1988 Count 90
- 8384.1 *Renia flavipunctalis* (Gey.)
July 24, 1989 Count 3
- 8386 *Renia adspersigillus* (Bosc)
June 29–Sep. 7, 1990 Count 14
- 8387 *Renia sobrialis* (Wlk.)
July 24, 1989–July 27, 1990 Count 3
- 8393 *Lascoria ambigualis* Wlk.
Aug. 14, 1989 Count 1
- 8397 *Paltis angulalis* (Hbn.)
May 30, 1991–Sep. 14, 1990 Count 39
- 8398 *Paltis asopialis* (Gn.)
June 6, 1991–Sep. 25, 1992 Count 33
- 8401 *Redectis vitrea* (Grt.)
July 17, 1992 Count 1
- 8404 *Rivula propinquialis* Gn.
May 30, 1991–Sep. 14, 1990 Count 21
- 8421 *Hypenodes fractilinea* (Sm.)
Aug. 27, 1992 Count 1
- 8427 *Dyspyralis puncticosta* (Sm.)
July 19, 1991 Count 1
- 8428 *Dyspyralis nigella* (Stkr.)
June 27, 1991–July 31, 1989 Count 3
- 8441 *Bomolocha manalis* (Wlk.)
June 15, 1990–Sep. 6, 1991 Count 11
- 8442 *Bomolocha baltimoralis* (Gn.)
May 30, 1991–Sep. 14, 1990 Count 131
- 8444 *Bomolocha palparia* (Wlk.)
July 8–July 29, 1988 Count 3
- 8445 *Bomolocha abalienalis* (Wlk.)
May 30–Aug. 30, 1991 Count 2
- 8446 *Bomolocha deceptalis* (Wlk.)
June 26–Sep. 9, 1989 Count 11
- 8447 *Bomolocha madefactalis* (Gn.)
June 12–Aug. 21, 1989 Count 9
- 8465 *Plathyphenia scabra* (F.)
May 30, 1991–Sep. 25, 1992 Count 37
- 8479 *Spargaloma sexpunctata* Grt.
June 12, 1992–Aug. 24, 1990 Count 8
- 8491 *Ledaea perditalis* (Wlk.)
Aug. 21, 1989 Count 1
- 8499 *Metalectra discalis* (Grt.)
July 5, 1991–Aug. 21, 1989 Count 4
- 8514 *Scolecocampa fiburna* (Gey.)
July 5, 1991–Aug. 14, 1989 Count 15
- 8536 *Calyptra canadensis* (Bethune)
June 15, 1988–July 4, 1989 Count 4
- 8555 *Scoliopteryx libatrix* (L.)
June 13, 1991 Count 1
- 8587 *Panopoda rufinargo* (Hbn.)
May 30–Aug. 30, 1991 Count 57
- 8588 *Panopoda carneicosta* Gn.
July 12–July 19, 1991 Count 3
- 8641 *Drasteria grandirena* (Haw.)
July 10, 1989 Count 1
- 8689 *Zale lunata* (Drury)
June 29, 1988–July 19, 1991 Count 2
- 8692 *Zale galbanata* (Morr.)
June 12, 1989 Count 1
- 8695 *Zale undularis* (Drury)
June 26, 1989–July 8, 1988 Count 3
- 8697 *Zale minerea* (Gn.)
May 30, 1991–July 15, 1988 Count 20
- 8704+ *Zale helata* (Sm.)
June 19, 1989 Count 1
- 8716 *Zale unilineata* (Grt.)
May 18, 1988–June 26, 1992 Count 13
- 8717 *Zale horrida* Hbn.
June 19, 1989 Count 2
- 8719 *Euparthenos nubilis* (Hbn.)
June 12, 1989–Aug. 16, 1991 Count 11
- 8721 *Allotria elonympha* (Hbn.)
June 12, 1989–July 19, 1991 Count 6

8727	<i>Parallela bistriaris</i> Hbn. June 12, 1989–Aug. 19, 1988	Count 13	8955	<i>Marathyssa inficita</i> (Wlk.) June 26, 1989–Aug. 19, 1988	Count 6
8738+	<i>Caenurgina crassiuscula</i> (Haw.) July 8–Sep. 24, 1988	Count 10	8957	<i>Paectes oculatrix</i> (Gn.) June 8–Aug. 9, 1990	Count 11
8745	<i>Mocis texana</i> (Morr.) June 15, 1988	Count 1	8968	<i>Eutelia pulcherrima</i> (Grt.) June 1, 1990	Count 1
8747	<i>Celiptera frustulum</i> Gn. June 19, 1989	Count 1	8970	<i>Baileya ophthalmica</i> (Gn.) May 30, 1991–Aug. 16, 1990	Count 14
8778	<i>Catocala habilis</i> Grt. July 26, 1991–Sep. 2, 1989	Count 3	8971	<i>Baileya dormitans</i> (Gn.) May 28, 1992–Sep. 7, 1990	Count 49
8779	<i>Catocala serena</i> Edw. Sep. 9, 1989	Count 2	8972	<i>Baileya levitans</i> (Sm.) June 1–July 27, 1990	Count 12
8785	<i>Catocala residua</i> Grt. Aug. 7, 1989–Sep. 25, 1992	Count 3	8973	<i>Baileya australis</i> (Grt.) July 8, 1988–July 10, 1989	Count 2
8788	<i>Catocala resecta</i> Grt. Aug. 24–Sep. 21, 1990	Count 6	8983	<i>Meganola minuscula</i> (Zell.) June 8–June 22, 1990	Count 4
8795	<i>Catocala palaeogama</i> Gn. July 19, 1991–Sep. 10, 1992	Count 20	8983.1	<i>Meganola phylla</i> (Dyar) June 5–June 12, 1992	Count 2
8797	<i>Catocala subnata</i> Grt. July 29, 1988–Sep. 4, 1992	Count 3	8990	<i>Nola cilicoides</i> (Grt.) May 30, 1991	Count 1
8798	<i>Catocala neogama</i> (J.E. Smith) Aug. 5, 1988–Sep. 21, 1990	Count 9	9037	<i>Hyperstrotia pervertens</i> (B. & McD.) June 6, 1991–July 24, 1989	Count 29
8801	<i>Catocala ilia</i> (Cram.) July 8–Sep. 24, 1988	Count 11	9040	<i>Hyperstrotia secta</i> (Grt.) June 26, 1989–July 13, 1990	Count 5
8802	<i>Catocala cerogama</i> Gn. July 29, 1988–Sep. 9, 1989	Count 9	9047	<i>Lithacodia muscosula</i> (Gn.) May 30, 1991–Aug. 27, 1992	Count 26
8803	<i>Catocala relicta</i> Wlk. Aug. 5–Sep. 10, 1988	Count 4	9048	<i>Lithacodia albida</i> (Gn.) July 3, 1992–July 26, 1991	Count 3
8805	<i>Catocala unijuga</i> Wlk. July 22, 1988	Count 1	9051	<i>Lithacodia musta</i> (G. & R.) July 19, 1991–Sep. 7, 1990	Count 2
8834	<i>Catocala amatrix</i> (Hbn.) Sep. 21, 1990	Count 1	9053	<i>Pseudeustrotia carneola</i> (Gn.) May 30, 1991–Sep. 10, 1988	Count 239
8846	<i>Catocala sordida</i> Grt. July 29, 1988–July 31, 1989	Count 3	9055.1	<i>Maliattha synochitis</i> (G. & R.) May 30, 1991–July 24, 1992	Count 28
8857	<i>Catocala ultronia</i> (Hbn.) July 19, 1991–Sep. 9, 1989	Count 28	9057	<i>Homophoberia apicosa</i> (Haw.) Aug. 19, 1988	Count 1
8858	<i>Catocala crataegi</i> Saund. July 8–Aug. 5, 1988	Count 6	9062	<i>Cerna cerintha</i> (Tr.) May 30, 1991–July 24, 1989	Count 12
8863	<i>Catocala mira</i> (Grt.) July 29, 1988–Aug. 21, 1989	Count 8	9065	<i>Leuconycta dipteroides</i> (Gn.) June 6, 1991–Aug. 21, 1989	Count 19
8864	<i>Catocala grynea</i> (Cram.) July 19, 1991–Sep. 9, 1989	Count 21	9090	<i>Tarachidia candefacta</i> (Hbn.) June 5, 1992–Sep. 10, 1988	Count 36
8867	<i>Catocala blandula</i> Hulst July 15, 1988	Count 1	9095	<i>Tarachidia erastrioides</i> (Gn.) June 12, 1989–Aug. 31, 1990	Count 18
8878.1	<i>Catocala lineella</i> Grt. July 31–Sep. 9, 1989	Count 5	9182	<i>Panthea furcilla</i> (Pack.) June 29–Aug. 24, 1990	Count 8
8887	<i>Trichoplusia ni</i> (Hbn.) Sep. 13, 1991	Count 1	9185	<i>Colocasia propinquilinea</i> (Grt.) May 14–July 24, 1989	Count 64
8898	<i>Allagrapha aerea</i> (Hbn.) May 30, 1991–Sep. 7, 1990	Count 20	9189	<i>Charadra deridens</i> (Gn.) Aug. 14, 1989	Count 1
8899	<i>Pseudeva purpurigera</i> (Wlk.) July 3, 1992–July 13, 1990	Count 3	9193	<i>Raphia frater</i> Grt. June 15, 1988–July 10, 1989	Count 10
8908	<i>Autographa precationis</i> (Gn.) May 25, 1988–Sep. 25, 1992	Count 30	9200	<i>Acronicta americana</i> (Harr.) June 6, 1991–July 24, 1989	Count 27
8924	<i>Anagrapha falcifera</i> (Kby.) May 28, 1992–Sep. 21, 1990	Count 19	9203	<i>Acronicta dactylina</i> Grt. July 27, 1990	Count 1
8952	<i>Plusia contexta</i> Grt. Sep. 21, 1990	Count 1	9219	<i>Acronicta connecta</i> Grt. Aug. 24, 1990	Count 1

9229	<i>Acronicta hasta</i> Gn. June 8–Aug. 24, 1990.....	Count 16
9235	<i>Acronicta spinigera</i> Gn. May 21, 1989–July 22, 1988.....	Count 26
9236	<i>Acronicta morula</i> G. & R. May 30, 1991.....	Count 2
9237	<i>Acronicta interrupta</i> Gn. Aug. 24, 1990.....	Count 1
9238	<i>Acronicta lobeliae</i> Gn. Aug. 7, 1992.....	Count 1
9243	<i>Acronicta ovata</i> Grt. June 15, 1988–Aug. 7, 1992.....	Count 7
9244	<i>Acronicta modica</i> Wlk. June 15, 1988–June 26, 1989.....	Count 3
9245+	<i>Acronicta haesitata</i> (Grt.) May 30, 1991–July 22, 1988.....	Count 70
9251	<i>Acronicta retardata</i> (Wlk.) June 12, 1989–June 27, 1991.....	Count 6
9254	<i>Acronicta afflicta</i> Grt. June 22, 1988.....	Count 1
9258	<i>Acronicta sperata</i> Grt. June 1, 1990.....	Count 1
9261	<i>Acronicta impressa</i> Wlk. June 8, 1988–Aug. 3, 1990.....	Count 2
9272	<i>Acronicta obliuina</i> (J.E. Smith) Aug. 3, 1990.....	Count 1
9280	<i>Simyra henrici</i> (Grt.) June 1, 1990.....	Count 1
9285	<i>Polygrammate hebraeicum</i> Hbn. June 15–July 29, 1988.....	Count 13
9301	<i>Eudryas grata</i> (F.) June 6, 1991–Aug. 9, 1990.....	Count 46
9314	<i>Alypia octomaculata</i> (F.) July 15, 1988.....	Count 1
9328	<i>Apamea nigrior</i> (Sm.) June 26, 1992.....	Count 1
9329	<i>Apamea cariosa</i> (Gn.) Aug. 5, 1988–Aug. 9, 1990.....	Count 4
9331	<i>Apamea cristata</i> (Grt.) July 5, 1991.....	Count 1
9344	<i>Apamea plutonia</i> (Grt.) June 15, 1988.....	Count 1
9348	<i>Apamea amputatrix</i> (Fitch) July 24, 1989.....	Count 1
9364	<i>Apamea sordens</i> (Hufn.) June 1, 1990–June 15, 1988.....	Count 2
9367	<i>Apamea dubitans</i> (Wlk.) July 27–Sep. 7, 1990.....	Count 4
9391	<i>Luperina passer</i> (Gn.) July 6, 1990.....	Count 1
9404	<i>Oligia modica</i> (Gn.) July 20, 1990–Sep. 6, 1991.....	Count 19
9406	<i>Oligia fractilinea</i> (Grt.) June 12, 1992–Sep. 2, 1989.....	Count 6
9410	<i>Oligia crytora</i> (Franc.) June 22, 1988.....	Count 1
9419	<i>Oligia mactata</i> (Gn.) Sep. 24, 1988.....	Count 3
9427	<i>Meropleon diversicolor</i> (Morr.) Aug. 9–Sep. 7, 1990.....	Count 3
9453	<i>Celaena reniformis</i> (Grt.) Sep. 9, 1989–Sep. 21, 1990.....	Count 2
9454	<i>Amphipoea velata</i> (Wlk.) June 20, 1991–Aug. 5, 1988.....	Count 69
9457+	<i>Amphipoea americana</i> (Speyer) July 6, 1990–Aug. 5, 1988.....	Count 9
9463	<i>Parapamea buffaloensis</i> (Grt.) Aug. 26, 1988.....	Count 1
9471	<i>Papaipema arcivorens</i> Hamp. Sep. 7, 1990–Sep. 13, 1991.....	Count 2
9483	<i>Papaipema inquaesita</i> (G. & R.) Sep. 10, 1988–Sep. 21, 1990.....	Count 4
9485	<i>Papaipema baptisiae</i> (Bird) Sep. 7, 1990–Sep. 24, 1988.....	Count 5
9505	<i>Papaipema cerussata</i> (Grt.) Sep. 24, 1988.....	Count 2
9509	<i>Papaipema unimoda</i> (Sm.) Aug. 19–Sep. 24, 1988.....	Count 5
9520	<i>Achatodes zae</i> (Harr.) July 15, 1988–Aug. 7, 1992.....	Count 5
9545	<i>Euplexia benesimilis</i> McD. May 30, 1991–Aug. 31, 1990.....	Count 45
9546	<i>Phlogophora iris</i> Gn. June 15, 1988–July 17, 1989.....	Count 4
9547	<i>Phlogophora periculosa</i> Gn. Aug. 14, 1989–Sep. 10, 1988.....	Count 52
9555	<i>Ipiomorpha pleonectus</i> Grt. Aug. 5, 1988–Sep. 7, 1990.....	Count 2
9556	<i>Chytonix palliatricula</i> (Gn.) June 6, 1991–July 31, 1992.....	Count 21
9578	<i>Hyppa xylinoidea</i> (Gn.) May 28, 1989–Aug. 27, 1992.....	Count 28
9582	<i>Nedra ramosula</i> (Gn.) Aug. 2, 1991–Sep. 2, 1989.....	Count 2
9618	<i>Phosphila turbulenta</i> Hbn. July 24, 1989–July 29, 1988.....	Count 2
9631	<i>Callopietria mollissima</i> (Gn.) June 12–Aug. 21, 1989.....	Count 23
9638	<i>Amphipyra pyramioides</i> Gn. July 31, 1989–Sep. 25, 1992.....	Count 80
9647	<i>Atheris miranda</i> (Grt.) June 12, 1989–Aug. 24, 1990.....	Count 3
9650	<i>Anorthodes tarda</i> (Gn.) May 28, 1989–Sep. 10, 1988.....	Count 15
9661	<i>Crambodes talidiformis</i> Gn. July 10, 1989.....	Count 1
9662	<i>Balsa malana</i> (Fitch) June 15, 1988–Aug. 14, 1989.....	Count 4
9663	<i>Balsa tristrigella</i> (Wlk.) May 30, 1991–July 10, 1992.....	Count 8
9664	<i>Balsa labecula</i> (Grt.) June 22, 1988–July 24, 1992.....	Count 7
9666	<i>Spodoptera frugiperda</i> (J.E. Smith) Sep. 7–Sep. 21, 1990.....	Count 14
9669	<i>Spodoptera ornithogalli</i> (Gn.) Aug. 26, 1988–Sep. 14, 1990.....	Count 3

9678	<i>Elaphria versicolor</i> (Grt.) June 26, 1989–July 15, 1988	Count 4
9681	<i>Elaphria festivoides</i> (Gn.) June 15, 1990–July 10, 1992	Count 7
9688	<i>Galgula partita</i> Gn. June 8, 1990–Sep. 13, 1991	Count 18
9689	<i>Perigea xanthoides</i> Gn. June 6, 1991–Sep. 9, 1989	Count 6
9690	<i>Condica videns</i> (Gn.) July 29, 1988	Count 1
9696	<i>Condica vecors</i> (Gn.) June 1–Aug. 24, 1990	Count 15
9720	<i>Ogdoconta cinereola</i> (Gn.) June 12, 1989–Sep. 13, 1991	Count 12
9815	<i>Cosmia calami</i> (Harv.) July 12, 1991–July 31, 1992	Count 6
9818	<i>Anolita fessa</i> Grt. July 27, 1991–July 10, 1989	Count 3
9886	<i>Lithophane patefacta</i> (Sm.) Sep. 21, 1990	Count 1
9889	<i>Lithophane petulca</i> Grt. Sep. 21, 1990	Count 1
9957	<i>Smira bicolorago</i> (Gn.) Sep. 21, 1990–Sep. 25, 1992	Count 16
9961	<i>Anathix ralla</i> (G. & R.) Aug. 5, 1988–Sep. 25, 1992	Count 164
9989	<i>Sutyna privata</i> (Wlk.) Sep. 7, 1990	Count 1
10059	<i>Homohadena badistriga</i> (Grt.) Sep. 27, 1991–July 8, 1988	Count 2
10202	<i>Cucullia convexipennis</i> G. & R. July 4–Aug. 21, 1989	Count 2
10276	<i>Polia imbrifera</i> (Gn.) June 20, 1991–July 15, 1988	Count 11
10288+	<i>Polia detracta</i> (Wlk.) May 30, 1991–Aug. 5, 1988	Count 271
10292	<i>Melanchra adjuncta</i> (Gn.) June 22–Aug. 19, 1988	Count 7
10293	<i>Melanchra picta</i> (Harr.) July 26, 1991–Aug. 31, 1990	Count 2
10299	<i>Lacanobia subjuncta</i> (G. & R.) June 8, 1988	Count 1
10300	<i>Spiramater grandis</i> (Gn.) Aug. 30, 1991	Count 1
10304	<i>Trichordestra legitima</i> (Grt.) Aug. 14, 1989	Count 1
10368	<i>Lacinipolia meditata</i> (Grt.) Aug. 7, 1992	Count 1
10397	<i>Lacinipolia renigera</i> (Steph.) May 30, 1991–Sep. 24, 1988	Count 124
10405	<i>Lacinipolia lorea</i> (Gn.) June 6, 1991–July 4, 1989	Count 17
10436	<i>Aletia oxygala</i> (Grt.) Aug. 31–Sep. 7, 1990	Count 4
10438	<i>Pseudaletia unipuncta</i> (Haw.) Aug. 14, 1989–Sep. 25, 1992	Count 109
10440	<i>Leucania linita</i> Gn. July 19–July 26, 1991	Count 2
10444+	<i>Leucania phragmatidicola</i> Gn. June 12, 1992–Sep. 24, 1988	Count 35
10446+	<i>Leucania multilinea</i> Wlk. May 30, 1991–Sep. 2, 1989	Count 21
10447	<i>Leucania commoides</i> Gn. July 19, 1991–Aug. 9, 1990	Count 4
10461+	<i>Leucania ursula</i> (Fbs.) May 30, 1991–Sep. 14, 1990	Count 208
10495+	<i>Orthosia hibisci</i> (Gn.) May 21, 1989	Count 3
10501	<i>Crocigrapha normani</i> (Grt.) May 14, 1989–June 8, 1990	Count 25
10521	<i>Morrisonia confusa</i> (Hbn.) May 28–June 4, 1989	Count 3
10521.1	<i>Morrisonia latex</i> (Gn.) May 30, 1991–July 17, 1992	Count 45
10524	<i>Nephelodes minians</i> Gn. Aug. 26–Sep. 24, 1988	Count 18
10532	<i>Homorthodes furfurata</i> (Grt.) June 27, 1991–Aug. 7, 1992	Count 40
10578	<i>Pseudorthodes vecors</i> (Gn.) June 4, 1989–Sep. 10, 1988	Count 59
10585	<i>Orthodes crenulata</i> (Butler) June 8, 1988–Sep. 7, 1990	Count 11
10587	<i>Orthodes cynica</i> Gn. May 30, 1991–July 31, 1992	Count 321
10627	<i>Tricholita signata</i> (Wlk.) June 27, 1991–Sep. 24, 1988	Count 5
10663	<i>Agrotis ipsilon</i> (Hufn.) May 30, 1991–Sep. 25, 1992	Count 121
10674+	<i>Feltia subgottica</i> (Haw.) July 31, 1989–Aug. 30, 1991	Count 16
10676	<i>Feltia lerilis</i> (Grt.) July 31, 1989–Sep. 13, 1991	Count 11
10698.2	<i>Trichosilia geniculata</i> (G. & R.) Sep. 7, 1990	Count 1
10705	<i>Euxoa messoria</i> (Harr.) July 10, 1992	Count 1
10793	<i>Euxoa scholastica</i> McD. June 20, 1991–July 31, 1989	Count 4
10803	<i>Euxoa velleripennis</i> (Grt.) Sep. 9, 1989	Count 2
10891	<i>Ochropleura plecta</i> (L.) May 18, 1988–Sep. 9, 1989	Count 137
10903+	<i>Eugrotis illapsa</i> (Wlk.) June 22, 1990–Aug. 30, 1991	Count 2
10915	<i>Peridroma saucia</i> (Hbn.) July 17, 1989–Sep. 24, 1988	Count 8
10942.1+	<i>Xestia dolosa</i> Franc. May 30, 1991–Sep. 25, 1992	Count 857
10943	<i>Xestia normaniana</i> (Grt.) Aug. 5, 1988–Sep. 14, 1990	Count 116
10944	<i>Xestia smithii</i> (Snell.) Aug. 19, 1988–Sep. 25, 1992	Count 22
10950+	<i>Xestia bicarnea</i> (Gn.) Aug. 16, 1990–Sep. 10, 1988	Count 28
10955	<i>Xestia badinodis</i> (Grt.) Sep. 21, 1991–Sep. 24, 1988	Count 3

11000	<i>Anaplectoides prasina</i> (D. & S.) July 31, 1989	Count 1	11010	<i>Heptagrotis phyllophora</i> (Grt.) June 22, 1988	Count 1
11006	<i>Protolampra brunneicollis</i> (Grt.) June 15, 1988–Aug. 31, 1990	Count 9	11029+	<i>Abagrotis alternata</i> (Grt.) June 29, 1990–Sep. 25, 1992	Count 81
11007+	<i>Eueretagrotis signoides</i> (Gn.) June 20, 1991	Count 1	11068	<i>Helicoverpa zea</i> (Boddie) Sep. 9, 1989–Sep. 21, 1990	Count 16

KIRTLANDIA®

The Cleveland Museum of Natural History

December 1999

51:99-104

PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

PRESENTATION OF THE AWARD

MIRIAM SMEAD

*Trustee, The Cleveland Museum of Natural History
1 Wade Oval Drive, University Circle
Cleveland, Ohio 44106-1767*

We have gathered tonight to pay tribute to the world's foremost authority on the chimpanzee, Dr. Jane Goodall. In over thirty-five years of patient observation at the Gombe Game Reserve in East Africa, she has reached across eons of time to our evolutionary past and completely changed our understanding of the most intelligent of the great apes. Stephen Jay Gould, who received this award in 1993, has noted that Jane Goodall's work with chimpanzees is one of the world's great scientific achievements.

Jane Goodall was born in London, England. Her father was an engineer; her mother an internationally known novelist. As a child she had a great fascination for animals. Her dream was to someday go to Africa to study animals. In 1957 that opportunity arose. She was invited to visit a friend's parents' farm in Kenya. She worked diligently to earn her passage. At the age of twenty-three she left England by ocean liner for Mombasa on the East African coast. Following the visit, she set off for Nairobi to find the famed anthropologist Louis Leakey.

Dr. Leakey was greatly impressed by this young woman's intense interest in animals and hired her as an assistant secretary. In time he gained great confidence in her abilities and was impressed by her endless patience. He

encouraged this young woman, who had no formal training, to begin a long-term study of the chimpanzees in the jungles of Africa. Little did he know how gifted she would become at communicating with these non-human primates.

Thus, in July of 1960, with her beloved mother as her companion, Jane Goodall began over a quarter century of observations and discoveries of man's closest relative at the Gombe Game Reserve (now Gombe National Park). This was the beginning of the longest continuous field study of animals in their natural habitat.

In 1962, with Leakey's urging, she began work toward a Ph.D. at Cambridge University. In 1965 she was awarded her doctorate in ethology. She became the eighth person in the history of Cambridge to be awarded a Ph.D. without having first earned a bachelor's degree.

She returned to Africa to found the Gombe Stream Research Center. Her work continues there today, through the efforts of her research team, providing insights into the lives of non-human primates. The scientific world, at first critical of her research methodology, today lauds her approach of patient observation, of letting the chimpanzees tell about themselves. Today her method is the standard used by fellow ethologists.

*On April 18, 1997, the David S. Ingalls, Jr. Award for Excellence was presented to Jane Goodall. A slightly shortened version of Miriam Smead's speech on that occasion is printed here. Jane Goodall's remarks, which follow on p. 103-104, are excerpted from her acceptance speech.

Through the years Dr. Goodall's research and fascinating discoveries have become known to the world through many avenues: her writings, television appearances, National Geographic articles, and documentaries. She is the author of four books for adults and two for children. Through her books, *In the Shadow of Man* (1971), *The Chimpanzees of Gombe* (1986), and *Through a Window* (1990), she has enchanted us with her anecdotes about her Gombe chimps. We have met and come to know the individuals whose lives she has observed. We now understand that they have behavioral patterns, cognitive abilities, emotions like our own with the capacity for affection and tenderness, and that they are capable of making and using tools. And yes, like us, they also have a dark side to their nature and can be just as brutal as humans. Through her books that mirror chimpanzee life, we see our own lives reflected and become starkly aware of how closely we are related.

In 1977 she established the Jane Goodall Institute for Wildlife Research, Education, and Conservation. Based in Silver Spring, Maryland, it promotes animal research throughout the world, and provides support for research on wild chimpanzees. It also provides funding for sanctuaries in a number of African locations for the humane, long-term care of orphaned chimpanzees. Tragically, increased demand for them, not only by scientists, but by circuses, zoos and film studios, has resulted in an increase of illegal trade in these primates.

Aware that field research must be augmented by conservation education to preserve wild chimpanzees and their habitats, she began a "Roots and Shoots" program in Africa as an effort to involve young people in conservation. In 1993 Dr. Goodall and a delegation of children made an appearance at the United Nations Environmental Conference. Following this the "Roots and Shoots" movement spread to many countries throughout the world.

She is the founder of "ChimpanZoo," a program for students, keepers, and volunteers to study chimpanzee behavior in zoo groups. Such programs have helped to greatly improve chimpanzee life in zoos, with larger enclosures, more nutritious food, and activities to help dispel boredom.

With grave concerns for the dwindling populations of chimpanzees, in 1986 she helped found the Committee for the Conservation and Care of Chimpanzees. She lobbied the United States government to give added protection to chimpanzees by reclassifying them as "endangered" rather than as "threatened species." By appearing on prime television programs she has helped to educate the public concerning conservation issues.

Another concern has been the treatment of chimps and other animals in today's medical research practices. She is dedicated to making improvements in this area. As our ambassador for the chimpanzees, her plea in her own words is, "Surely we must speak for them - for they cannot speak for themselves."

Dr. Goodall has been the recipient of numerous scientific awards: the National Geographic Society's Hubbard Medal,



Jane Goodall, April 18, 1997.

the Golden Medal of Conservation from the San Diego Zoological Society, the Kilimanjaro Medal for Wildlife Conservation Prize, and the J. Paul Getty Wildlife Conservation Prize, to name a few. This Museum's David S. Ingalls, Jr. Award for Excellence is awarded to an individual for excellence in research, education or conservation in one of the fields of natural science represented by The Cleveland Museum of Natural History. The individual chosen will have made a major contribution that is recognized by the national or international scientific community.

Dr. Jane Goodall, we are indeed indebted to you, not only for the more than thirty-five years in which your gift of communication with the chimpanzees has dispelled myths and revealed profound scientific discoveries, but also for your ability to communicate and share with us the excitement and the truths of your research. In so doing you have won countless numbers of human supporters of all ages for these non-human primates, our closest relatives.

It is my distinct honor, on behalf of the Board of Trustees of The Cleveland Museum of Natural History, to present to you the David S. Ingalls, Jr. Award for Excellence.

INTRODUCING JANE GOODALL

WILLIAM C. MCGREW

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On Monday, April 14th, 1997, *USA Today* reported that the most popular American television commercial of 1997 so far, as determined by reader survey, is an HBO commercial featuring Jane Goodall and the chimpanzees of Gombe. Upon reading this, I could only smile and shake my head: firstly, because I was in Kigoma, Tanzania, when the HBO film crew passed through town and so wondered what they were up to, and secondly, because it showed yet again that when tonight's recipient puts her mind to a project, it will have an impact.

I feel honored to be asked to introduce Jane Goodall this evening, but I also feel daunted. After all, we have known one another for more than a quarter of a century, yet the organizers of this evening's ceremonies told me to confine my remarks to only 10 minutes, 15 at the most! So, from the many lives of Jane Goodall, I have chosen just three: Jane Goodall as scientist, Jane Goodall as educator, and Jane Goodall as conservationist. This omits several other aspects, admittedly, but then, any one of these three could have taken up all the time allotted!

Jane Goodall as scientist must be, first and foremost, the main reason that we are assembled here at one of the nation's most renowned natural history museums. And, even if our recipient had never inspired a single student nor saved a single ape, her place tonight would be secure for her research and scholarship alone. She is, I suspect, the most widely-known and respected woman scientist in the world. Yet she got to be that way by a most unorthodox route: She never went to a university as an undergraduate; her mentor, Louis Leakey, who sent her out to do field work, was a prehistorian and not a primatologist; and instead of joining an established research team at a well-known field site, she was sent to start from scratch, accompanied by her mother! (Although anyone who knows Vanne Goodall will realize what a happy choice that was!) To pile one metaphor upon another, Jane Goodall was thrown in at the deep end and made to re-invent the wheel when it came to field primatology.

The result? The person who had never seen a wild chimpanzee when she began in July, 1960 at the Gombe Stream Reserve in western Tanzania, became the world's expert on the species in less than a decade. How that came about would take a lecture in itself, but by 1963 she had told us of chimpanzees being hunters and sharers of meat and, a year later, she revealed ape technology in a masterly little letter to *Nature*. Then she was off to the University of Cambridge to tackle a Ph.D. with one of the world's foremost ethologists, Robert Hinde, and the resulting thesis became her comprehensive monograph on the lives of Gombe's chimpanzees, published in 1968. Scores of articles in learned jour-

nals and chapters in edited volumes followed, but her *magnum opus* appeared in 1986, *The Chimpanzees of Gombe*, published by Harvard University Press, all 673 pages of it, became the "bible" for chimpanzee. No other primatologist, before or since, has produced such a volume.

What makes her science so good? I suggest three elements. First, she took careful note of the spontaneous acts of individuals, and I stress that last word. From the time that the apes could be identified, she perceived them as individuals, refusing to lump them by age, sex, or rank. In effect, she "listened" to what each chimpanzee had to say and came to understand their rich social world accordingly. Second, she persevered. Jane committed herself and her colleagues, Tanzanians and expatriates, to the long-term study of an organism whose life span is measured in decades. This now amounts in some cases (most famously with the "F" family) to four generations of chimpanzees. Third, she never permitted herself to become ensnared in dogma. She went to Gombe with an open mind and kept it open. If the chimpanzees showed her infanticide and cannibalism as well as maternal devotion, then she reported it all. When after almost 15 years of apparently harmless though noisy threats and displays, the apes showed her inter-community warfare that led even to fatality, then she duly expanded her conception of chimpanzee nature.

What about Jane Goodall as educator? She has never held a permanent faculty position and so has never officially supervised a graduate student, yet her influence on learners has been immense. At a recent Wenner-Gren Foundation conference on The Great Apes, 21 primatological experts convened. These were the world's finest researchers on gorillas, orangutans, and bonobos, as well as chimpanzees. Fully a third of them, 7 in all, had worked with Jane at Gombe. Jane has mentored undergraduates, graduate students, and post-doctoral fellows, who are now to be found at the nation's best institutions of higher learning. Any one of us could stand here this evening and tell you of the crucial nature of Jane's contribution to our intellectual development at Gombe.

Yet, Jane Goodall's pedagogy goes far beyond the halls of academe. As early as 1967, she had begun to educate the general public, with the publication of *My Friends, the Wild Chimpanzees*, which grew out of her National Geographic articles and television documentaries. She broke new ground, sometimes astonishingly so. In 1971, her obituary for old Flo, the matriarch of the Gombe chimpanzees, was published in the *Sunday Times*. She wrote not one, but two best-selling popular accounts of Gombe: *In the Shadow of Man* in 1971, covered Gombe's first 10 years, and *Through a Window* in 1990, chronicled the next 15 years.

Yet, as an academic, I must return to what may be Jane's most significant, yet least recognized, impact, that of an educator. In 1997, one of my students at Miami University, Amy McClain, undertook a project to assess the extent of Jane Goodall's influence at large. She combed through 40 introductory college textbooks, meticulously noting every mention of chimpanzees. Jane's presence was ubiquitous — whether in anthropology, biology, or psychology, Jane Goodall was chimpanzees. She was cited even more often in cultural anthropology textbooks (a field of the discipline supposedly restricted to human beings) than in biological anthropology textbooks! In terms of the dissemination of knowledge in the widest sense, she is surely primatology's answer to Margaret Mead.

Jane Goodall spends most of her waking hours these days as a conservationist and campaigner on behalf of the welfare and preservation of chimpanzees, both in captivity and in nature. This is most readily seen in the fund-raising and speaking engagements that go to support the Jane Goodall Institute for Wildlife Research, Education and Conservation, with its variety of activities worldwide. Most direct of these are the refuges, or sanctuaries, in countries like Congo, Tanzania, Kenya and Uganda, that take in confiscated, orphaned or abandoned chimpanzees. On another front, she

founded ChimpanZoo, a consortium of North American zoos who through collective research on their charges have raised the consciousness of keepers and administrators to the conditions of confinement. Elsewhere, Jane is committed to Roots and Shoots, her conservation organization focused on young people, now in the process of being expanded to include college students. It is no accident that its motto is: "Every individual can make a difference." Her writing reflects these applied interests. Goodall's 1993 book, *Visions of Caliban*, written with Dale Peterson, recounts the complex and sometimes painful relations between humans and their ape cousins.

Some people have questioned Jane Goodall's now overriding commitment to conservation, but it seems a perfectly straight-forward development: in coming to know another species, you come to value it, and if that means working to save it, then so be it. Besides, Jane Goodall has always been a conservationist. Does anyone really believe that Gombe Stream Reserve would have been upgraded to a national park in 1968, had she not done chimpanzee research there?

So, my time is up, although there is still much more that could be said, but I think you've heard enough from me. I am pleased to be able to say a few words about such a scientist, educator, conservationist, and friend of all chimpanzees everywhere, Dr. Jane Goodall.

REPLY

JANE GOODALL
Jane Goodall Institute
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Thank you, what an honor to be here and to receive this wonderful, prestigious prize. And thank all of you for coming to share this special moment. Standing up here now in front of you all I can't help but be reminded of an old Texas saying, "If you see a turtle on top of a 10-foot pole you sure as heck know she didn't get there by herself." As one climbs up the ten foot pole of life, indeed there are so many people to provide help and support. I've been incredibly fortunate during my life to have had all those students, people like Bill McGrew and Linda, who helped to collect the data over the years, the wonderful Tanzanian field staff, and all the staff of the Jane Goodall Institute.

Of all the people who helped me throughout my life, colleagues and friends, scientists, and just ordinary people out there, the one that I feel I owe the most to is my mother. I told her this morning that I was getting this award, and she wished she could be here. She is 93 years old now and she is as sharp as she ever was. Right from the beginning she has been there to support and help. When I had taken a whole handful of earthworms up to bed when I was just eighteen months old, she didn't say "yuck," and throw them out of the window. She said, "Jane, if you leave them here they will soon be dead." So, I ran with them into the garden. A few years later, I went off to spend time with my father's family in the country. Here's this little girl from a city, loving animals, who is suddenly out in the fields among the cows, the pigs and the horses. One of my jobs, as I went through these marvelous learning days, was to help collect the hens' eggs. As I collected the eggs and put them in my basket, I began to be curious. There's the egg, so where is the hole in the hen big enough for that egg to come out of? I couldn't see it. I kept asking everyone and nobody obviously told me to my satisfaction, so I decided, in my little four-and-a-half-year-old mind, that I had to find out by myself. I saw a hen walking up the gang plank to her little wooden house and I crawled after her. She flew out. So, I hid in the back of the hen house and I waited and I waited. My father's family called the police. And as dusk was falling, and my mother was still out searching, she suddenly saw this little creature rushing toward the house, covered in straw. She didn't grab, as so many mothers would, and ask, "Where have you been? Don't you know how worried we have been?" She saw my excitement and sat down to hear the wonderful story of how a hen lays an egg.

As soon as I began to read, I wanted to read books about animals. Dr. Doolittle was one of my early childhood heroes. Then I met Tarzan, and by the time I was eight or nine I was madly in love with him and terribly jealous of Tarzan's Jane. I thought that I would have made a much better mate for Tarzan myself. So, by this time I was dreaming about going to Africa, of living with animals, and writing books about them. My family had no money, my father was off fighting in the war. My mother's friends apparently kept saying to her, "Why don't you tell Jane to dream about something she can achieve? She'll never get to Africa." But you see, this remarkable mother used to say to me, "Jane, if you really want something, and if you take advantage of opportunity, if you never give up, you'll find a way." So, the way I found is history. I worked as a waitress saving up the wages and the tips, and I received that wonderful letter inviting me to Africa. I set off at the age of twenty-three on this big ship, by myself, to stay with my school friend. That was when I heard about Louis Leakey.

Every time I come to a place like this, I sort of go back to those early days in Kenya, to Louis Leakey and the natural history museum in Nairobi. I could answer most of the questions he asked me about the animals. That's why he gave me a job. Then he allowed me to go with his wife and one other young English girl and himself, of course, to Olduvai Gorge. In those days Olduvai wasn't known at all because no human fossilized remains had been found, so there was no road, there was no trail, there was nothing.

Everyday after the hard work of chipping away under the hot sun, we were allowed to go out on the plains, and in those days there were so many animals: the giraffes, the zebras, and the antelopes. And one evening there was a rhino, and two young male lions that followed us curiously about, which was a little bit frightening—but just magic. I wonder if you can imagine what it was like for this young girl who had dreamed of Africa all her life. Every morning when I woke up, I was in my dream, and my dream was suddenly a reality. I think that's when Louis Leakey decided I was the person he had been looking for, to go and try and find out about our closest living relative.

He was far ahead of his time, a giant and genius of a man, another of the great inspirational forces in shaping my career. He argued that if we found behavior that was common to

humans today and chimpanzees today, that behavior may well have been present in an apelike, humanlike creature that led to the stock leading to today's chimpanzees and humans. If behavior common to chimpanzees and humans today was present in the common ancestor millions of years ago, then probably we could guess what has happened in our own earliest known ancestors. And so this was Louis Leakey's argument, and as Bill so eloquently said, there are very few textbooks today that deal with human evolution that don't mention chimpanzee behavior to some extent. They usually specifically mention the Gombe chimpanzees, so Louis was tremendously vindicated.

It wasn't very easy to get the money for me to go there. I was untrained as you've heard, and who was going to give him money? In those days young people, especially young women, did not go tramping off into the forest living with animals. Moreover, I didn't have any kind of university education; but finally Louis found a wealthy American business man who provided money for six months. It still wasn't the end of Louis' problems, because in those days Tanganyika was a British protectorate. British authorities found a young girl on her own in the bush to be preposterous. However, Leakey never gave up, eventually he persuaded them to allow me to go, providing I took a companion. That was when my mother volunteered to accompany me. She stayed for three months.

Looking back over these 37 years, back over the facts that have been related to you tonight, teaching us about our closest living relatives, I think the thing that is the most striking is the ways in which they do so much resemble us. Yes, there are all the biological similarities, the close resemblance in the structure of the blood and the immune system and the fact that the chimpanzee brain and central nervous system is more like ours than that of any other creature. The fact that the DNA of chimpanzees and humans differs by only just over one percent. These are only interesting to the scientists, particularly those working on medical research. These researchers are trying to learn about the nature of certain diseases which chimpanzees, because they are so like us, can be infected with.

It was rather tragic that for so long, the behavioral similarities that are logically to be expected from those similarities in the brain and central nervous system were denied. That is what enabled chimpanzees in medical laboratories around the world to be confined in tiny cages for a life span that may be up to sixty years. Research on the Gombe chimpanzees showed them to have vivid personalities, and tool using and cooperative behavior. Their nonverbal communication patterns—kissing, embracing, holding hands, patting on the back, swaggering, and threatening—are so like ours.

So in all these ways we find the chimpanzees resembling us far more than anybody had thought. And should it surprise us that they also have emotions similar to ours? Given these

similarities, along with the similar brain and central nervous system, I don't think so. This leads to ethical problems, when we then consider how we use and abuse so many of these amazing non-human beings, often without really thinking of what we are doing. Knowing all of this about the chimpanzees, how tragic to find that they are disappearing so fast in Africa due to habitat destruction and to the increased numbers of the human population and to logging.

If we look around the world today, we can see cruelty, not only to the chimpanzees and other animals, but the cruelty that we inflict on each other. We can see massive deforestation going on, not only in the developing world, but also in the last remaining forests and woodlands of North America and Europe. We can look at the rate of the spread of deserts as a result of deforestation. We can look at the pollution, sometimes massive pollution. I think the question I get asked most often is, "Jane, do you think there's hope?"

I have three reasons for hope and I'd like to end up by sharing those three reasons with you. The first lies in the incredible brain that each one of us is endowed with. Even though we're so close biologically to chimpanzees, the intellectual performances of the human really do dwarf those of even the most gifted of chimpanzees, and there are some very gifted chimpanzees. So, given this amazing brain, don't you think we can get together around the world and start healing the scars and finding ways of living in better harmony with nature? This leads into my second reason for hope, which is that, as young people around the world get more and more educated, so does their commitment and energy for conservation become enormous. There's a wonderful energy in young people and this is what led me to develop the Roots and Shoots Program. Roots creep under the ground to make firm foundations; shoots seem small, but to reach the light they can break brick walls. Let's think of the brick walls as all those problems that I already mentioned. The message of Roots and Shoots is one of hope. Hundreds and thousands of Roots and Shoots, young people from preschool to universities around the world, together can break through, can change the course of the planet today.

My final reason for hope is human spirit. As I travel around the world, I meet people who are so truly remarkable, people who tackle problems they're told are impossible, but who will succeed or blaze the trail for others to follow. People who overcome the most amazing disabilities, physical disabilities or what have you, and somehow lead a life that is a shining example to those around them. I traveled around the world with a few symbols of hope. Just at supper time today, I asked for something that would be a symbol of hope for Cleveland. I had heard about Lake Erie and the surrounding rivers and the fire hazards that were there not so very long ago. Now the water is much cleaner. So Aaron gave me a little piece of driftwood that he collected from the lake as a symbol of hope for Cleveland. This also shows the amazing recuperative power of nature, if we give her a chance.



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The Scientific Publication of The Cleveland Museum of Natural History

Joseph T. Hannibal, Editor

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ON THE IDENTITY OF *ARCHIULUS?* *GLOMERATUS* SCUDDER, 1890, A SUPPOSED MILLIPED (DIPLOPODA: XYLOIULIDAE) FROM THE PENNSYLVANIAN OF ILLINOIS

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ABSTRACT

One of the two syntypes of the species *Archilus? glomeratus* Scudder, 1890, is a xyloiulid millipede, but the other specimen belongs to the syncarid crustacean species *Acanthotelson stimpsonii* Meek and Worthen, 1865. The millipede is designated the lectotype of the species, which is assigned tentatively to the genus *Xyloiulus* Cook, 1895.

Introduction

The history of the study of fossil myriapod arthropods is replete with misidentifications at high taxonomic levels. This is understandable, as millipeds and centipeds superficially resemble other taxa, especially those with coiled parts or which bear a series of similar-looking segments.

When coiled or preserved as single segments, fossil millipeds may resemble plant parts. This has led to several specimens of fossil ferns being described as millipeds. *Palaeojulus dyadicus* Geinitz, 1872, a supposed millipede, was reinterpreted as a fern soon after its description (Scudder, 1886b, p. 17), as were Samuel Scudder's species of the supposed myriapod genus *Trichiulus* Scudder, 1884 (Scudder, 1886a; Scudder 1886b, p. 17). More recently, Hoffman (1969, p. R605) identified the supposed millipede *Julopsis cretacea* Heer, 1874, as a fern.

Myriapods have also been confused with various other

types of segmented animals, including annelid worms, onychophorans, and arachnids. Scudder (1882a) identified *Palaeocampa* Meek and Worthen, 1865, which was originally described as a caterpillar, as a myriapod. Later Fritsch (1907) reinterpreted *Palaeocampa* as a polychaete annelid. Recent authors have come to the same conclusion (Hoffman, 1969, p. R605; Rolfe et al., 1982; Fitzhugh et al., 1997). *Ilyodes* Scudder, 1890a, was originally described as a chilopod, but was subsequently identified as an onychophoran by Rolfe et al. (1982; see also Hay and Kruty, 1997, p. 217). *Necrogammarus salweyi* Woodward, 1870, a form that had been referred to as an early myriapod, has only recently been identified as a eurypterid (Selden, 1986).

Fossils of Crustacea with multiple abdominal and thoracic segmentation often bear a close resemblance to fossil myriapod arthropods. Both types of arthropods are also often found in the same rock units. Thus it is not surprising

that Scudder assigned a number of crustacean specimens to two "species" of his supposed chilopod genus *Eileticus* Scudder, 1882b. Hoffman (1969, p. R604) noted that this genus was based on "purported myriapod remains." However, Brooks (1962, p. 258) considered the holotype of *Eileticus anthracinus* Scudder, 1882b, to be a fossil of a typical myriapod and Shear (1997, p. 213), citing Mundel (1979), recently noted that *Eileticus* may be a geophilomorph. Mundel (1979, p. 377) had referred to possible chilopod material which included *Eileticus* (?) *antiquus* Matthew, 1894. That material, however, is in need of reevaluation. Both Brooks (1962, p. 258) and Schram (1984, p. 207) considered the material referred to *Eileticus* by Scudder (1890a, 1890b), with the exception of the holotype of *Eileticus anthracinus*, to belong to the syncarid *Acanthotelson stimpsonii* Meek and Worthen. The case of *Eileticus* is complex; more information on the recent history of the taxonomy of the genus can be found in Brooks (1962) and Schram (1984).

Scudder was not the only worker who may have confused Crustacea with myriapod arthropods. Anton Fritsch briefly described a "lithobiid?" (1910, p. 7) specimen from the Cretaceous of the Czech Republic, noting that interpretation of this specimen was difficult. He did not name this species. Fritsch's figure (1910, Pl. 4, fig. 12) of this specimen resembles that of a crustacean. Unfortunately, the specimen itself, which is preserved in the collections of the Národní Muzeum, Prague, is too poorly preserved for identification.

The purpose of this paper is to illustrate and redescribe the syntypes of *Archilius? glomeratus* Scudder, 1890a, and to designate a lectotype so as to resolve the taxonomic placement of the species. This is necessary as the syntypes belong to two different classes of arthropods.

Scudder referred two specimens from the Mazon Creek fauna to this new "archipolypod" species *Archilius? glomeratus* in 1890. He described one specimen as a "moderately large galley-worm" [millipede] with 18 or 19 segments and long, stout, legs. The other, which he was "inclined to place in the same species" was a smaller, but seemingly more complete, specimen. One of these two specimens (the "moderately large galley-worm") is, in fact, a syncarid crustacean, complete with a raptorial appendage. That specimen is partly coiled, only superficially resembling a coiled millipede. The other specimen of *Archilius? glomeratus*, which Scudder was "inclined to place in the same species," is in fact a coiled, cylindrical, helminthomorph millipede.

Systematic Paleontology

Class MALACOSTRACA Latreille, 1806

Subclass EUMALACOSTRACA Grobben, 1892

Order SYNCARIDA Packard, 1885

Suborder PALAEOCARIDACEA Brooks, 1962

Family ACANTHOTELSONIDAE Meek and Worthen, 1865

Genus *ACANTHOTELSON* Meek and Worthen, 1865

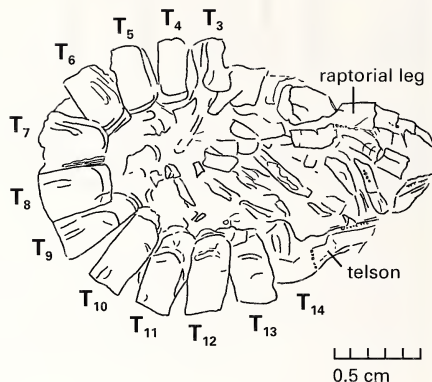


Figure 1. *Acanthotelson stimpsonii* Meek and Worthen, 1865, paralectotype of *Archilius? glomeratus* Scudder, 1890a, USNM 37993. Camera lucida drawing of part of specimen seen in Figure 2A, with several parts identified; T = thoracomere.

Diagnosis

"Second and third thoracopods raptorial. Telson and uropods styliform." (From Schram, 1984, p. 205.)

ACANTHOTELSON STIMPSONII Meek and Worthen, 1865
Figures 1–2

Acanthotelson Stimpsonii MEEK AND WORTHEN, 1865, p. 47–48.

Acanthotelson Stimpsoni MEEK AND WORTHEN, 1866, p. 401, Pl. 32, fig. 6; MEEK AND WORTHEN, 1868, p. 549–550, figs. a–b; WHITE, 1884, p. 176–177, Pl. 37, figs. 4–5.

Acanthotelson stimpsoni SCHRAM, 1984, p. 205–207, fig. 9, Pl. 1, figs. c–e, Pl. 2, fig. a; SCHRAM, ROLFE, AND HAY, 1997, p. 158, figs. 12.8–12.9.

Acanthotelson Eveni MEEK AND WORTHEN, 1868, p. 551, figs. a–d; WHITE, 1884, p. 177–178, Pl. 38, figs. 4–7.

Eileticus anthracinus SCUDDER, 1890a, p. 420–421, Pl. 38, fig. 5; SCUDDER, 1890b, p. 396–397, Pl. 30, fig. 5.

Eileticus aequalis SCUDDER, 1890a, p. 421, Pl. 38, figs. 6–9; SCUDDER, 1890b, p. 397, Pl. 30, figs. 6–9.

Archilius? glomeratus SCUDDER, 1890a, p. 436–437, Pl. 37, fig. 2; SCUDDER, 1890b, p. 412–413, Pl. 29, fig. 2 (new synonymy).

Archilius glomeratus SCUDDER, 1891, p. 10 (in part; new synonymy).

For additional synonyms see Schram, 1984, p. 205–206.

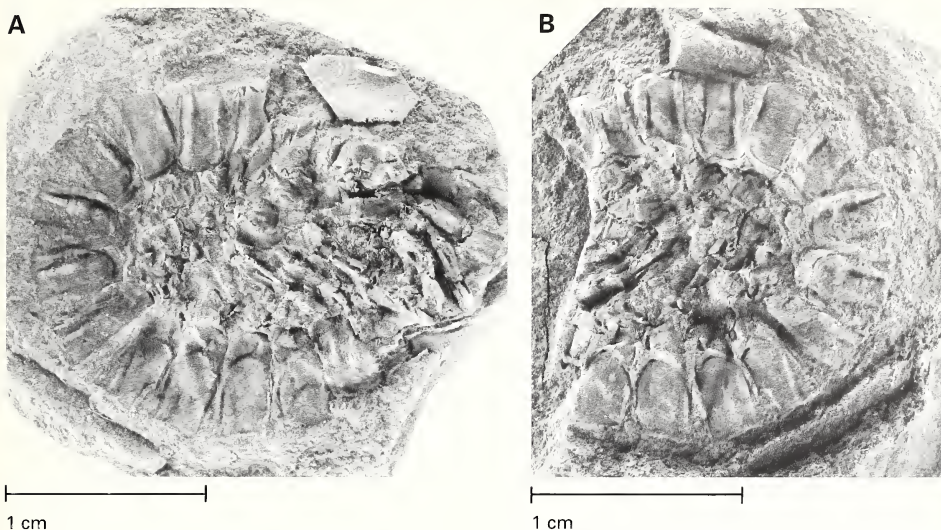


Figure 2. *Acanthotelson stimpsonii* Meek and Worthen, 1865, paralectotype of *Archinus?* *glomeratus* Scudder, 1890a, USNM 37993. A, remains preserved in one half of concretion; B, remains preserved in other half of concretion.

Material studied

USNM 37993; collected by J. C. Carr, originally numbered 1823a/b in the Lacoe Collection (Scudder, 1890a, p. 437; Scudder, 1890b, p. 413). Collected at Mazon Creek, Grundy Co., Illinois, from the Francis Creek Shale, Westphalian D in age. Preserved in concretion.

Description of specimen

Moderate size for species. Cephalon incomplete. Third through 14th thoracomeres more or less well preserved. Average dimensions of thoracomeres 2 mm long and 4 mm high; first three preserved thoracomeres increasing gradually in size. Posterior of 14th thoracomere spinous. Presumed antennal peduncle with spine bases along length and at points of articulation. Raptorial leg prominent, spinose. Walking legs robust. Telson and uropods probably styliform, with spines of varying sizes along length.

Remarks

Three species belonging to the family Acanthotelsonidae are found in the Mazon Creek fauna: *Acanthotelson stimpsonii* Meek and Worthen, 1865; *Palaeocaris typus* Meek and Worthen, 1865; and *Palaeosyncaris micra* Schram, 1984. The seemingly styliform telson and uropods of the specimen described above indicate that it belongs to the species *A. stimp-*

sonii. The specimen also displays the stout raptorial spines of that species (Meek and Worthen, 1868, p. 551b, d [identified as *Acanthotelson Eveni*]; Brooks, 1962, text plate 11, fig. a). In addition, the specimen can be distinguished from the other two Mazon Creek species as it lacks the enlarged sixth thoracomere found in *P. typus* and the posterior of its 14th thoracomere is spinose, unlike the smooth posterior of that thoracomere in *P. micra*.

Scudder's description of *Archinus?* *glomeratus* was published in the *Memoirs of the Boston Society of Natural History* (Scudder, 1890a) and in *Fossil Insects of North America* (Scudder, 1890b) in the same year. It is difficult to determine which publication has priority, but Scudder himself listed the Boston Society publication first in his list of citations to *A. glomeratus* in his index to fossil insects (Scudder, 1891, p. 10) and other authors have generally done the same. Regardless of priority, both publications are virtually identical.

As *Acanthotelson stimpsonii* has recently been restudied, only an abbreviated synonymy is provided above. Additional synonyms can be found in Schram (1984, p. 205–206).

The spelling *A. stimpsonii*, as originally used by Meek and Worthen (but later abandoned by the authors) appears to be the genitive of the Latinized form of Stimpson so must be revived as the correct spelling according to Article 33.4 of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1999).

Scudder's two specimens of the species *Archiliulus? glomeratus* Scudder, 1890a, have been considered cotypes (Schuchert, 1905, p. 61), that is syntypes. Scudder emphasized the specimen described above (which is a crustacean) in his original description, describing it first and in greater detail than the other specimen he referred to his supposed species of milliped. However, Scudder did not specifically refer to the specimen he emphasized as the type. For the sake of maintaining a stable concept of the species, I am designating the other specimen of the syntype series, which is a true milliped, as the lectotype of the species *Archiliulus? glomeratus* Scudder, 1890a. And I am designating the crustacean specimen (USNM 37993) as the paralectotype of the species *Archiliulus? glomeratus* Scudder, 1890a.

This partly coiled crustacean specimen does resemble a myriapod in side view, especially as seen in Scudder's figure (1890a, Pl. 37, fig. 2; 1890b, Pl. 29, fig. 2). Because of its rounded pleurites it bears a general resemblance to the milliped *Pleurojulus* Fritsch, 1899, which has recently been identified from the Mazon Creek fauna (Hannibal, 1996). However, the crustacean can easily be distinguished from a milliped based on its robust appendages and telson.

Acanthioteson stimpsonii is one of the most abundant species of fossil crustacean (Brooks, 1962, p. 230), as well as the most completely known of any fossil syncarid (Schram, 1986, p. 87). This species is most abundant in the Braidwood assemblage of the Mazon Creek fauna (Schram, Rolfe, and Hay, 1997, p. 158). Meek and Worthen published figures of *A. stimpsonii* (1866, Pl. 32; 1868, Pl. 38) that included both outstretched and partially coiled specimens. These figures were widely known and recopied (e.g., Lesley, 1889, p. 2). Nevertheless, Scudder was unable to recognize material belonging to this taxon. This might have been due to his unfamiliarity with fossil Crustacea from Mazon Creek, and in the case of USNM 37993, the relatively poor preservation of the anterior of the specimen.

Scudder's figured specimens of *Eileticus anthracinus* (in part) and *E. aequalis* (1890a, Pl. 38; 1890b, Pl. 30) are of outstretched specimens of *Acanthioteson stimpsonii* Meek and Worthen; this difference led him to distinguish these specimens from the coiled specimens he referred to *Archiliulus? glomeratus* Scudder, 1890a. Thus, Scudder's failure to notice the similarity of some of his supposed myriapod material with that of Meek and Worthen's crustacean material resulted in at least two species (assuming that the holotype of *E. anthracinus* is a milliped, but that assumption is in need of investigation) of myriapod arthropod being named based at least in part on material that can be assigned to a single species of crustacean.

Class DIPLOPODA Blainville in Gervais, 1844
Subclass HELMINTHOMORPHA Pocock, 1887
Order ?SPIROBOLIDA Bollman, 1893
Family XYLOIULIDAE Cook, 1895a

Discussion

Hoffman (1963) included the Archiulidae of Scudder (1873) in part, the Xyloiulidae of Cook (1895a, 1895b), and the Projulidae of Fritsch (1899) in this family.

?XYLOIULUS GLOMERATUS (Scudder, 1890a)

Figure 3

Archiliulus? glomeratus SCUDDER, 1890a, p. 437, Pl. 37, fig.

3; SCUDDER, 1890b, p. 413, Pl. 29, fig. 3.

Archiliulus glomeratus SCUDDER, 1891, p. 10 (in part).

Material studied

USNM 37994; originally numbered 1823c/d in the Lacoe Collection (Scudder 1890a, p. 437; Scudder, 1890b, p. 413). Collected at Braidwood, Illinois, from the Francis Creek Shale, Westphalian D in age. Preserved in concretion. Composed of natural molds, with some pyritic ?replacement or cast material present.

Description of specimen

Elongate, cylindrical milliped. About 40 segments exposed, length of exposed portions about 33 mm, maximum height of body about 2.5 mm. Tapers toward posterior. Separation of prozonites and metazonites indistinct. Pleurotergites marked with fine longitudinal striae, composed of series of grooves and ridges. Eight to ten striae per 0.5 mm. Striae cross most of pleurotergite but more prominent toward middle and posterior. Striae on middle and upper part of pleurotergites curve toward dorsum anteriorly.

Remarks

Scudder (1890a, p. 437; 1890b, p. 413) described this specimen second in his description of the species *Archiliulus? glomeratus* and was only "inclined to place" it in the same species as the first specimen. While most of the body is preserved, neither the anteriormost nor the posteriormost part of the body is evident, only parts of the proximal leg segments are represented, and the preservation of the specimen is only of mediocre quality. Despite these factors, I am designating this specimen, which is a true milliped, as the lectotype of *Archiliulus? glomeratus* Scudder. This is being done for the sake of avoiding confusion and for maintaining nomenclatorial stability.

Although recent works (Hannibal, 1997) on the Mazon Creek fauna have noted the presence of xyloiulids, there has been little detailed work on xyloiulids since the work of Scudder (e.g., Scudder, 1873) and, more recently, Hoffman (1963, 1969). Scudder (1873, p. 239) noted the resemblance of *Archiliulus* Scudder, 1868 (proposed in Dawson, 1868, p. 495, 496), and *Xylobius* Dawson (= *Xyloiulus* Cook, 1895a), distinguishing *Archiliulus* by its lack of "frustra" (= striae; see also Hoffman, 1963, p. 169) and other characters. Scudder's published figures (1890c; also published in Dawson, 1878, p.

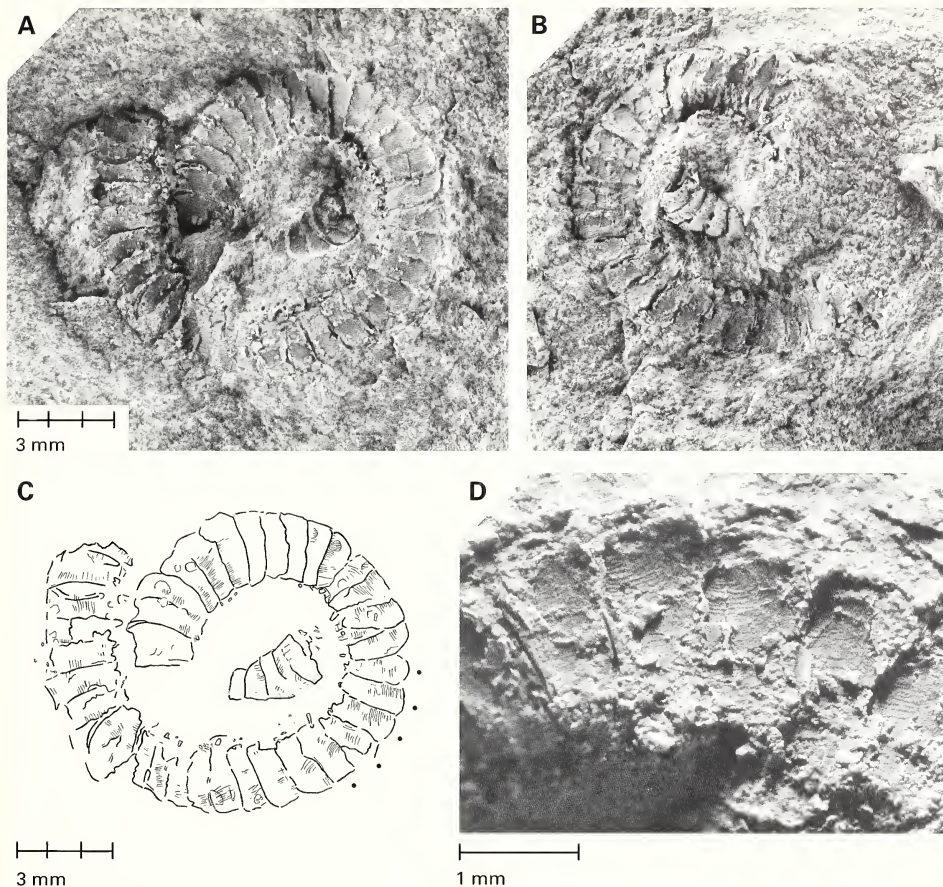


Figure 3. ?*Xyloilulus glomeratus* (Scudder, 1890a), lectotype of *Archilus? glomeratus* Scudder, 1890a, USNM 37994. A, remains preserved in one half of concretion; B, remains preserved in other half of concretion; C, camera lucida drawing of part of specimen seen in A, dots indicate segments seen in D; D, close-up of natural mold of several segments showing striae, composed of series of grooves and ridges.

56) illustrating differences between *Xylobius* (= *Xyloilulus*) and *Archilus* show little detail, but his illustrations indicate that there are more striae on the segments of *Xyloilulus* than on those of *Archilus*. Thus *Archilus? glomeratus* is tentatively assigned to the genus *Xyloilulus* Cook, 1895a, rather than to the genus *Archilus* Scudder, 1868. The species appears to have the characters of the genus *Xyloilulus* as diagnosed by Hoffman (1963, p. 171). However, the assignment

is tentative as the longitudinal grooves of the species are not distinctly continuous along the entire length of the segments as they are in certain *Xyloilulus*.

Scudder (1890a, p. 438–440; 1890b, p. 414–416) described two species of *Xyloilulus*, *Xyloilulus frustulentus* (Scudder) and *Xyloilulus mazonus* (Scudder), from Mazon Creek. Without reexamination of the type material, these species can be compared to ?*Xyloilulus glomeratus* only in

gross respects. Based on Scudder's descriptions ?*Xyloilulus glomeratus* is most like *Xyloilulus frustulentus*. Both ?*Xyloilulus glomeratus* and *Xyloilulus frustulentus* are small xyloilulids and both have closely spaced striae. According to Scudder, however, *X. frustulentus* has alternating longer and shorter segments. These appear to be lacking in ?*Xyloilulus glomeratus*. Scudder's illustrations of *Xyloilulus frustulentus* (Scudder, 1890a, Pl. 37, figs. 4-6; 1890b, Pl. 29, figs. 4-6) are inadequate for further comparison. Restudy of *Xyloilulus frustulentus* and comparison with ?*Xyloilulus glomeratus* is needed, but is beyond the scope of this paper.

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REEVALUATION OF THE FAMILY ATELECYCLIDAE (DECAPODA: BRACHYURA)

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ABSTRACT

All of the genera previously assigned to the Atelecyclidae Ortmann, *sensu lato* (Decapoda: Brachyura) have been systematically evaluated and assigned to appropriate families. In addition to systematic observations, a cladistic analysis was performed on the fourteen genera with recent representatives. The cladistic analysis supported the conclusions drawn from classical systematic observations in placing the genera into four separate families. Belliidae Guinot is comprised of *Bellia*, *Acanthocyclus*, *Corystoides*, and *Heterozius*. Thiidae Dana includes *Thia* and *Kraussia*. Cheiragonidae Ortmann embraces *Telmessus*, *Erinacrus*, and *Montezumella*. Atelecyclidae *sensu stricto*, consists of *Atelecyclus*, *Peltariou*, *Krunopeltariou*, *Pteropeltarion*, and *Trichopeltarion* (= *Trachycarcinus*). *Avitelnessus* has been assigned to the Dakotancruidae, *Cyclocancer* to the ?Cancridae, and *Pliosoma* to the Majidae.

A detailed systematic study of *Trichopeltariou greggi*, Miocene in age, was conducted based upon over 140 specimens. Comparisons between *T. greggi*, the closely allied species *Trichopeltarion fantasticum* (endemic to New Zealand), and other species assigned to *Trichopeltarion* and *Trachycarcinus* resulted in the synonymization of the two genera, resolving the longstanding debate of differentiating between them. Paedomorphism was suggested as a possible explanation for the variations in size, shape, and ornamentation that were used by previous authors to separate the two genera. Synonymizing *Trachycarcinus* with *Trichopeltarion* increases the number of species of *Trichopeltarion* in the fossil record from one to seven.

Introduction

The Atelecyclidae comprises a relatively small group of morphologically distinctive, dominantly deep-water crabs known from localities throughout the world. They are almost always rare elements in the modern biota. Atelecyclids are even less common in the fossil record. The entire fossil record of the family, as it is defined herein, consists of seven species in one genus. Despite the distinctiveness of authentic atelecyclids, many genera, properly belonging to other families, have been assigned to the family at one time or another.

This study investigates the taxonomy of fossil and living brachyuran crabs that at one time or another have been included in the Atelecyclidae. The fossils are mostly problematic, in part because the atelecyclid fossil record is quite poor, and because the placement of many of the supposed fossil representatives of the family is highly questionable.

A cladistic analysis of 14 extant genera has been utilized to improve the understanding of the phylogeny of the family, and to test the classical systematics. Thus, the purposes of this work are to define these crabs and their key characters, to summarize the complex history of their classification, to present a cladistic analysis of the extant genera, and to provide detailed systematic descriptions of taxa that have not been recently treated.

General Characteristics of Atelecyclidae

In the past, authors have associated the atelecyclids with the superfamilies Cancroidea, Brachyrrhyncha, and Corystoidea. Guinot (1989) placed the atelecyclids within the superfamily Corystoidea, Rathbun (1930b) placed them within the superfamily Brachyrrhyncha, and Glaessner (1969) placed Atelecyclidae in the section Cancridea. The relative placement of the genera within families and superfamilies has changed throughout taxonomic history and is extremely confusing.

Figure 1 provides a detailed schematic of brachyuran morphology.

As defined by Alcock (1899, p. 2–5) the tribe Cancroidea, or Cyclometopa, possesses the following characters: Carapace variable in shape, being broader than long, or longer than broad. Anterolateral margins generally arched, sometimes strongly. Posterolateral margins convergent, sometimes very strongly. Front broad and horizontally or obliquely deflexed. Front sometimes prominent, but never forms a pointed rostrum with the basal antennal joints for pillars as in spider crabs. Buccal orifice square cut, except in the Corystidae, where anterior angles may be rounded and convergent with anterior boundary being indefinite. Palp of external maxillipeds almost always articulates with anterointernal angle of merus. Epistome transverse, never long, sometimes linear and sunken, and indistinguishable in the Corystidae. Antennules fold, either transversely or longitudinally. Abdomen of male occupies all of space between last pair of legs. Genital ducts of male open on bases of last pair of legs.

Characters that have been used by Borradaile (1907, p. 481) and others to distinguish the atelecyclids from other cancrroid families are as follows: Body shapes of various families elongate-oval, wider than long, round, transversely oval, hexagonal, or subcircular. Orbits can be complete, or incomplete. Antennal flagella, when present, can be long and hairy or short and not hairy. Antennules may fold longitudinally or transversely. Presence or absence of a rostrum is used to distinguish between certain families. Fore edge of the mouth, or buccal frame, sharply cut in some families and indistinct in others. Location of articulation between carpus and merus of third maxillipeds is another distinguishing character, as is the presence of a lobe on the inner angle of the endopodite of the third maxillipeds. Other useful characters include: a) whether the eyes are unprotected or sheltered within the orbit, b) the degree to which the branchial region is swollen, c) the location of the male genital openings, and d) adaptation of the legs for swimming.

Characters that authors have used to designate subgroups within the Atelecyclidae have led to the establishment of subfamilies. Rathbun (1930b) separated the Atelecyclinae (= Atelecyclidae) from the Acanthocyclinae (= Belliidae) based on the following: The Atelecyclinae possess an antenna that succeeds the basal article that is stout and provided with a flagellum. Antennules fold within their cavity. Front, between the antennae, is cut into two, three, or four teeth, or is entire. The Acanthocyclinae have antennae that are rudimentary or absent. Antennules are stout and too large to retract within their cavity. Carapace rotund.

Sakai (1976, p. 306–316) used a classification system that separated the atelecyclids into two subfamilies, Atelecyclinae and Thiinae. The Atelecyclinae are defined as having a carapace that is suboval or oblong to pentagonal. Carapace regions are fairly well defined. Anterolateral margins usually bear teeth. Front cut into two, three, or four teeth. Movable part of antennal peduncle is well developed, stout, and provided with a flagellum. Basal segment of antenna either fixed or slightly movable. The Thiinae are defined by having a subcircular carapace that have regions which are not delimited. External maxillipeds entirely close buccal orifice. Anterolateral margins denticulate or entire. Front cut into two lobes, which may again be subdivided into two lobules. Basal joint of the antennae fixed.

While the aforementioned characters have been used previously to define groups, authors have used them in different combinations. This has led to varying classification systems which diagnose families and subfamilies differently. Thus, a new comprehensive diagnosis for the Atelecyclidae is warranted.

History of the Atelecyclidae

The genera that have been included in the Atelecyclidae have had a very complex history of classification. Early authors did not agree in taxonomic placement of the genera in question, nor did they always assign the same taxonomic

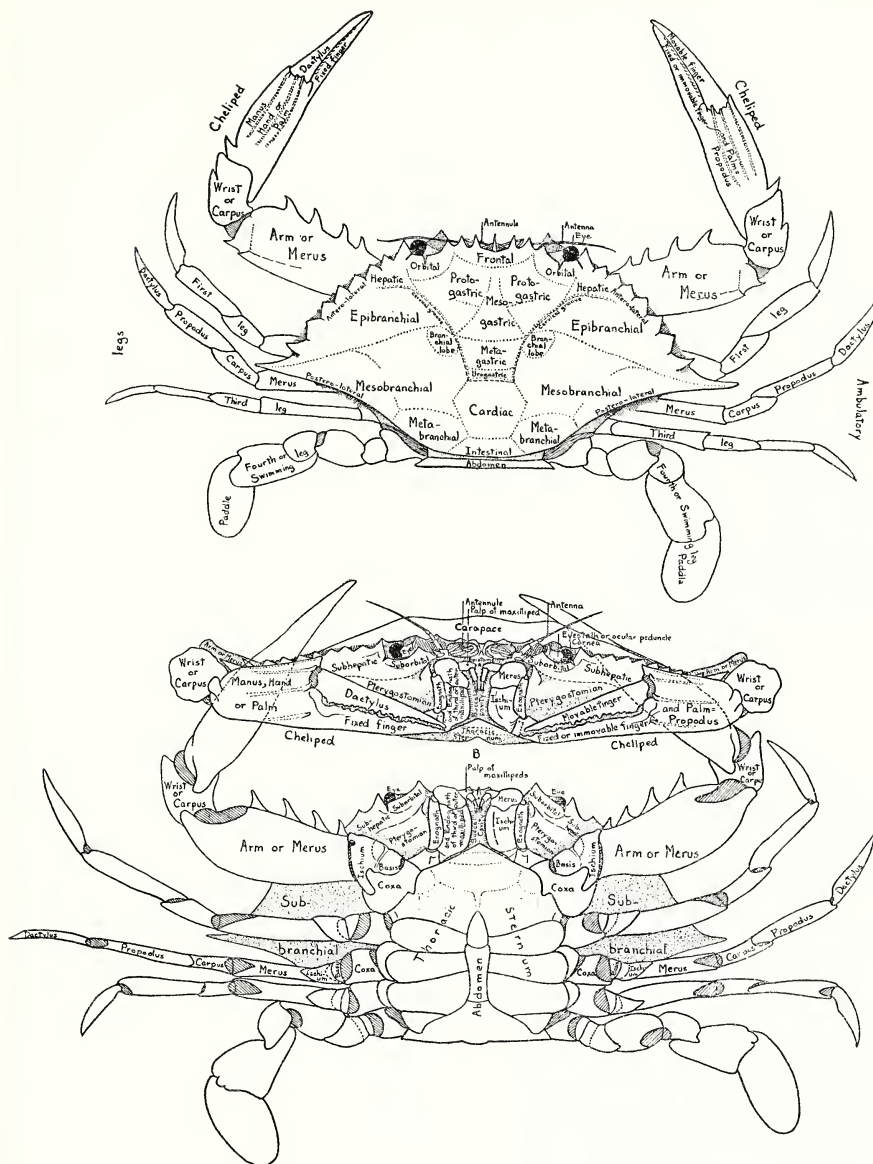


Figure 1. Dorsal (top), orbital (central), and ventral (bottom) views of a portunid crab showing terms used in descriptions. From Rathbun, 1930b.

Table 1. Classification systems of various authors. The genera considered in this study are set in boldface italics.

H. Milne Edwards and Lucas, 1843	Dana, 1852a	Miers, 1886	Ortmann, 1893	Alcock, 1899
Section Brachyura	Order Eubrachiata	Brachyura	Brachyura	Brachyura
Family Catometopes	Tribe Macroura	Natural Group Oxyrhyncha	Cancroidea	Tribe Cyclometopa (=Cancroidea)
Genus <i>Atelecyclus</i>	Tribe Anomoura	Natural Group Catometopa	Cyclometopa	Family Telphusidae
Genus <i>Acanthocyclus</i>	Subtribe Dromidea	Natural Group	Parthenopini	Family Xanthidae
Genus <i>Corystoides</i>	Subtribe Raminidea	Cyclometopa (=Cancroidea)	Family Pathenopidae	Family Portunidae
	Subtribe Bellidae	Legion Cancrinea	Family Eumendonidae	Family Corystidae
	Family Bellidae	Legion Telphusinea	Family Cheiragonidae	Genus <i>Corystes</i>
	Genus <i>Bellia</i>	Legion Corystoidea	Genus <i>Cheiragonus</i> (= <i>Telmessus</i>)	Genus <i>Corystoides</i>
	Genus <i>Corystoides</i>	Genus <i>Hypopeltarion</i> (= <i>Peltarion</i>)	Cancrini	Genus <i>Bellia</i>
	Tribe Brachyura	Genus <i>Gomezia</i>	Family <i>Atelecyclidae</i>	Genus <i>Gomezia</i>
	Subtribe Maiuidea	Legion Cyclinea	Genus <i>Atelecyclus</i>	Genus <i>Podocadactes</i>
	Subtribe Cancroidea	Genus <i>Acanthocyclus</i>	Genus <i>Hypopeltarion</i> (= <i>Peltariou</i>)	Genus <i>Nautilocorystes</i>
	Legion Cancrinea		Family Cancrinidae	Genus <i>Pseudocorystes</i>
	Legion Telphusinea			Family Cancrinea
	Legion Cyclinea			Subfamily Cancrinea
	Family Acanthocyclidae			Subfamily Pirimelinae
	Genus <i>Acanthocyclus</i>			Subfamily Thiinae
	Subtribe Corystoidea			Genus <i>Thia</i>
	Family Trichoceridae			Genus <i>Kraussia</i>
	Family Thiidae			Subfamily Atelecyclinae
	Genus <i>Thia</i>			Genus <i>Atelecyclus</i>
	Family Corystidae			Genus <i>Erimacrus</i>
	Genus <i>Corystes</i>			Genus <i>Hypopeltarion</i> (= <i>Peltariou</i>)
	Genus <i>Peltariou</i>			Genus <i>Pliosoma</i>
	Genus <i>Dicera</i>			Genus <i>Trichopeltarium</i> (= <i>Trichopeltariou</i>)
	Genus <i>Telmessus</i>			Genus <i>Trachycarcinus</i>
	Genus <i>Pseudocorystes</i>			Subfamily Acanthocyclinae
	Genus <i>Atelecyclus</i>			Genus <i>Acanthocyclus</i>
	Genus <i>Gomezia</i>			Subfamily Trichiinae
	Subtribe Grapsoidea			
	Subtribe Leucosoidea			

name or ranking to subdivisions of the Brachyura. The lack of uniform taxonomic designations leads to confusion when tracing the genera through their taxonomic histories. The systematic position of several genera continues to be in question. Many of the classification systems mentioned below are summarized in Table 1.

In 1843, Henry Milne Edwards and Lucas assigned *Atelecyclus* Leach, *Acanthocyclus* H. Milne Edwards and Lucas, and *Corystoides* H. Milne Edwards and Lucas to the family Catometopes. The family was placed in the section Brachyura.

In 1852a, 1852b, Dana considered Brachyura to be a tribe of the order Eubrachiata along with two other tribes, Anomoura and Macroura (Table 1). His Brachyura consisted of five subtribes: the Maiuidea, Cancrinea, Grapsoidea, Leucosoidea, and Corystoidea. The Cancrinea was composed of three legions: the Cancrinea, Telphusinea, and Cyclinea. The latter contained the genus *Acanthocyclus* as part of the family Acanthocyclidae. The subtribe Corystoidea consisted of three families:

Trichoceridae, Thiidae, and Corystidae. The latter contained two genera now referred to the Atelecyclidae, *Atelecyclus* Ortmann and *Peltarion* Jacquinot, and a third genus *Telmessus* White, now referred to the Cheiragonidae (Števcic, 1988). Other genera of the Corystidae included *Pseudocorystes* Edwards, *Gomezia* Gray, *Corystes* Latreille, *Oeidia* De Haan, and *Dicera* De Haan. At that time, the Corystidae embraced the genera now included within the Atelecyclidae. *Bellia* and *Corystoides* were placed in the Bellidae, but they were classified as anomourans. Today, these two genera are considered to be clearly Brachyura, not Anomoura.

Miers (1886) recognized natural groups of the Brachyura. His natural group Cyclometopa (= Cancroidea) contained four legions (Table 1). The Corystoidea legion contained the genus *Hypopeltarium*, which has since been synonymized with *Peltarion*. This was the only genus of the current atelecyclids recognized in Miers' classification system. He did, however, place *Acanthocyclus*, now a belliid, within the Cyclinea legion.

Table 1. Continued.

Borradaile, 1907	A. Milne Edwards and Bouvier, 1923	Rathbun, 1930b	Guinot, 1977
Suborder Brachyura	Brachyrhyncha	Tribe Brachyura	Brachyura
Subtribe Oxystomata	Cyclometopa	Subtribe Brachygnatha	Section Podotremata
Subtribe Dromiacea	Family Corystidae	Superfamily Brachyrhyncha	Section Heterotremata
Subtribe Brachygnatha	Genus <i>Corystoides</i>	Family Euryalidae	Superfamily Dorippoidea
Superfamily Oxyrhyncha	Genus <i>Peltarion</i>	Family Portunidae	Superfamily Calappoidea
(=Maiidea)	Genus <i>Trichopeltarion</i>	Family Cancridae	Superfamily Corystoidea
Superfamily Brachyrhyncha		Family Atelecyclidae	Genus <i>Corystes</i>
(=Cancridea)		Genus <i>Atelecyclus</i>	Genus <i>Pseudocorystes</i>
Family Corystidae		Genus <i>Telmessus</i>	Genus <i>Nautilocorystes</i>
Family Portunidae		Genus <i>Erimacrus</i>	Genus <i>Peltarion</i>
Family Potamonidae		Genus <i>Peltarion</i>	Genus <i>Trichopeltarion</i>
Family Xanthidae		Genus <i>Trichopeltarion</i>	Genus <i>Pteropeltarion</i>
Family Gonoplacidae		Genus <i>Trachycarcinus</i>	Genus <i>Trachycarcinus</i>
Family Ptenoplacidae		Genus <i>Pliosoma</i>	Genus <i>Atelecyclus</i>
Family Cancridae		Subfamily Acanthocyclinae	Genus <i>Thia</i>
Family Atelecyclidae		Genus <i>Acanthocyclus</i>	Genus <i>Cancer</i>
Subfamily Atelecyclinae		Genus <i>Bellia</i>	Genus <i>Perimela</i>
Subfamily Thiinae		Genus <i>Corysoides</i>	Genus <i>Stipus</i>
Subfamily Acanthocyclinae			Genus <i>Telmessus</i>
Family Palicidae			Genus <i>Erimacrus</i>
Family Grapsidae			Genus <i>Podocadactes</i>
Family Gecarcinidae			Superfamily Portunoidea
Family Ocypodidae			Superfamily Xanthoidea
			Superfamily Majoidea
			Superfamily Parthenopoidea
			Superfamily Bellioidea
			Superfamily Leucosioidea
			Section Thoracotremata

In 1893, Ortmann established the Atelecyclidae and placed it within the Cancrini along with the Cancrinidae and Cancridae (Table 1). He included the Cancrini and Parthenopini in the Cyclometopa, a subdivision of the Cancrinea legion. One genus contained within the Atelecyclidae was *Atelecyclus*, for which Ortmann recognized three species: *A. rotundus* Olivi, *A. septidentatus* Montagu, and *A. heterodon* Leach. All have since been synonymized into *A. rotundus*. *Hypopeltarion* (Miers), misspelled by Ortmann, was the other genus considered to be an atelecyclid.

In 1899, Alcock agreed with the limits placed on the Cyclometopa, or Cancroidea, by Miers (1886, p. 106), but did not agree with Miers' subdivision. Alcock also recognized Ortmann's natural classifications of 1893–94 and 1898 for Cyclometopa, but did not agree with the inclusion of the Parthenopidae and exclusion of the Corystidae. Alcock proposed that the Cyclometopa (Cancroidea) should contain the families Telphusidae, Xanthidae, Portunidae, Cancridae, and Corystidae (Table 1). The sub-

families proposed for the Cancridae were the Cancrinae, Pirmelinae, Thiinae, Atelecyclinae, Acanthocyclinae, and Trichiinae. Alcock's decisions regarding the subfamily Atelecyclinae and its defining characters have been followed by Rathbun (1930b) and Balss (1957).

Alcock's defining characters were as follows: Carapace subcircular, often a little longer than broad, regions usually well defined, not much areolated, anterolateral margins usually with teeth. Front usually cut into three (sometimes two or four) teeth which are often prominent. Buccal orifice elongate, not completely covered by the external maxillipeds which are elongate, especially the merus, and overlap or completely conceal the sunken epistome. Basal antennal joint either fixed or slightly movable. Those characters allowed the following genera to be included within the Atelecyclinae: *Atelecyclus*, *Erimacrus* Benedict, *Hypopeltarion*, *Pliosoma* Stimpson, *Telmessus* White, *Trachycarcinus* Faxon, and *Trichopeltarion* A. Milne Edwards.

Borradaile (1907, p. 467–486) proposed a key to the families of the decapod crustaceans. The classification system divided the Brachyura into three subtribes: the Oxystomata, Dromiacea, and Brachygnatha (Table 1). Within the key to the families of the Brachyryhyncha, the Atelecyclidae are joined with twelve other families by possessing complete orbits (though fissures may remain) where the eyes are almost or completely unprotected. The body is rarely elongate-oval, the rostrum is usually absent, and the second antennal flagellum is usually short, and not hairy.

The next set of characters in Borradaile's key encompasses the Atelecyclidae, Portunidae, Potamonidae, Cancridae, Xanthidae, and Gonoplacidae, and separates them from the other seven families of the Brachyryhyncha because they share the following characters: Carpus of third maxillipeds articulates at or near anterointernal angle of merus. Body usually round or transversely oval. Male openings nearly always coxal. In many species right chela always larger than left.

The next tier of characters separates the aforementioned families from the portunids: Legs not adapted for swimming, or, if so modified, then vas deferens (male sperm duct) opens sternally or extends in a sternal groove. Inner lobe on endopodite in the first maxillipeds lacking.

Next, the potamonids are removed from the atelecyclids, cancrids, xanthids, and goneplacids because the latter are all marine crabs that do not possess greatly swollen branchial regions. The atelecyclids and cancrids are next separated from the xanthids and goneplacids on the basis of having the antennules fold lengthwise as opposed to folding in a slanting or transverse manner.

Lastly, the atelecyclids differ from the cancrids on the basis of exhibiting a subcircular carapace, and second antennal flagellum that is either well developed and hairy or wanting, compared to having a broadly oval carapace and second antennae that are short and not hairy.

The Atelecyclidae is then subdivided into three subfamilies. The Acanthocyclinae have no apparent antennal flagella, an uncleft front, and a mouth covered by the third maxillipeds. The Thiinae and Atelecyclinae both have antennal flagella, but the Thiinae have regions that are not defined, third maxillipeds covering the mouth, and a front that is entire or lobed. Members of the Atelecyclinae have regions that are more or less marked out, third maxillipeds that do not cover the mouth, and a toothed front. The same classification of the Atelecyclinae and Acanthocyclinae within the Atelecyclidae was later used by Rathbun (1930a).

Subsequent to Borradaile, Alphonse Milne Edwards and Bouvier (1923) chose to put the genera *Peltarion*, *Trichopeltarion*, and *Corystoides* into the family Corystidae (Table 1).

Rathbun (1930b) followed the classification of Borradaile (1907). She divided the Atelecyclidae into the Atelecyclinae and the Acanthocyclinae (Table 1). The Acanthocyclinae, comprising *Acanthocyclus*, *Bellia*, and

Corystoides, is synonymous with the Belliidae Dana 1852a. Therefore, for Rathbun, the subfamily characteristics of Acanthocyclinae are those of the family Belliidae.

According to Guinot (1976, p. 15), and in reference to the Balss (1957) classification, *Bellia*, *Acanthocyclus*, *Corystoides*, and *Heterozius* A. Milne Edwards should be placed in the Belliidae and assigned to the superfamily Bellioidea, which would be at the same ranking as Oxxyrhyncha and Brachyryhyncha within the tribe Brachygnatha.

Rathbun's subfamily Atelecyclinae is therefore the closest synonym to the true atelecyclids. While many of the characters used by Rathbun (1930b, p. 148) to define the atelecyclids remain useful, others no longer may be considered definitive. The defining characters of the Atelecyclinae (Rathbun, 1930b) are as follows: Carapace suboval, oblong or pentagonal. Moveable part of the antennal peduncle well developed, stout, and provided with flagellum. Antennules fold normally within their cavity. Front, between antennae, cut into two, three, or four spines.

In 1977, Guinot proposed a new classification for the Brachyura, ranked at the infraorder level (Table 1). The classical taxa of the section level (Dromiacea, Oxystomata, Oxxyrhyncha, Cancridea, and Brachyryhyncha) were rejected and replaced by three new sections. The three new sections were created on the basis of the location of the female and male genital openings. The Podotremata have male and female coxal openings. Heterotremata have female sternal openings, and male openings that are coxal or sternal. Thoracotremata have male and female openings that are sternal.

A preliminary explanation for the subfamilies of this classification system is given by Guinot (1978). The tribe or group to which most of atelecyclid genera are assigned is the Corystoidea. Guinot cited the five corystoidean families of Bouvier (1942): the Corystidae (Corystinae and Atelecyclinae), Cancridae (= Cancrideae), Thiidae, Perimelidae (= Pirimelidae), and Belliidae (Bellidae). While the particular families that comprise the Corystoidea are not confirmed, the genera that she interpreted as belonging within this superfamily are given. These genera include *Corystes* Latreille, *Pseudocorystes* H. Milne Edwards, *Nautilocorystes* H. Milne Edwards, *Peltarion*, *Trichopeltarion*, *Trachycarcinus*, *Pteropeltarion*, *Atelecyclus*, *Thia*, *Cancer* Linné, *Perimela* Leach, *Sirpus* Gordon, *Podocercatodes* Ortmann, *Telmessus*, and *Erimacrus*.

The latter two genera were considered to have morphological differences warranting placement in a separate subfamily. *Telmessinae* Guinot, 1977, was proposed based upon the observation that the female sternum of *Telmessus* and *Erimacrus* is thickened and sculptured around the genital openings. In addition, the sixth abdominal segment is broadly incised, leaving the openings fully exposed. The establishment of this subfamily is not apparent, nor is the family to which it is assigned clear. Štefčić (1988) referred the genera *Telmessus* and *Erimacrus* to the Cheiragonidae.

Characters	Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14
		<i>Pliosoma</i>	<i>Erimacrus</i>	<i>Telmessus</i>	<i>Peltarion</i>	<i>Trichopeltarion</i>	<i>Trachycarcinus</i>	<i>Atelecyclus</i>	<i>Bellia</i>	<i>Acanthocyclus</i>	<i>Heterozius</i>	<i>Thia</i>	<i>Kraussia</i>	<i>Pteropeltarion</i>	<i>Krunopeltarion</i>
1. front		0	2	6	3	3	3	3	3	5	4	1	6	0	3
2. orbital direction		0	1	1	0	0	0	0	0	0	0	0	0	0	0
3. orbital makeup		0	0	0	0	0	0	0	0	1	1	0	1	0	0
4. antennae development		0	0	0	0	0	0	0	1	1	1	0	0	0	0
5. antennae direction		0	0	0	0	0	0	0	0	0	1	2	0	0	0
6. antennae folding		0	2	2	0	2	2	0	2	2	1	1	2	2	2
7. basal articles		0	1	1	0	0	0	0	0	0	2	0	0	0	0
8. antennule folding		0	0	0	0	0	0	0	2	2	1	1	1	0	0
9. antennule size		0	2	2	2	2	2	2	1	1	1	2	1	2	2
10. antennule cavity		0	1	1	1	1	1	1	2	2	1	1	1	1	1
11. eye length		0	1	1	0	0	0	1	1	1	1	1	1	1	0
12. eye retraction		0	0	0	0	0	0	0	1	0	0	0	0	0	0
13. canopy		0	1	1	1	1	1	1	0	0	1	1	0	1	1
14. body shape		0	7	3	4	4	4	4	2	6	6	5	5	3	1
15. lateral margins toothed		0	2	2	2	2	3	2	0	0	1	1	0	4	2
16. buccal region		0	0	0	0	0	0	0	0	3	3	0	0	0	0
17. anterior buccal limitation		0	1	2	1	1	1	1	1	0	0	1	0	1	1
18. buccal frame		0	0	0	0	1	1	1	0	0	0	0	0	1	1
19. sternal sutures		0	3	3	3	3	3	1	0	3	0	1	1	3	4
20. sternal shape		0	2	2	2	2	2	2	3	3	3	1	1	2	2

Figure 2. Matrix of characters used in the cladistic analysis and their corresponding character state numbers. The outgroup is assigned a state of "0" for each character.

Schweitzer and Salva (2000) reevaluated the Cheiragonidae and included within it the extinct genus *Montezumella*.

Since the work of Rathbun (1930b), there have been several works describing new species of *Trichopeltarion* (Richardson and Dell, 1964; Dell, 1968, 1969) and *Trachycarcinus* (Rathbun 1932; Sakai 1935, 1965; Guinot and Sakai 1970; Guinot 1986, 1989). Pequegnat (1970) proposed the synonymy of *Trachycarcinus spinulifer* with *Trichopeltarion nobile*. There has also been the identification of two new genera of atelecyclids, *Pteropeltarion* (Dell, 1972) and *Krunopeltarion* (Števíć, 1993). To date, however, the problem of the definition of the Atelecyclidae and the genera that should be included within it has not been resolved.

Geologic History of the Atelecyclidae

The Atelecyclidae, as treated herein, include the following genera: *Atelecyclus*, *Peltarion*, *Pteropeltarion*, *Krunopeltarion*, and *Trichopeltarion*. We synonymize *Trachycarcinus* with *Trichopeltarion*. Thus, all known fossil representatives of *Trachycarcinus* are assigned to *Trichopeltarion*.

The only genera to have a fossil record are *Trichopeltarion* and *Atelecyclus*. At this time, however, the identification of fossil representatives of *Atelecyclus* is under question (see p. 49). Therefore the lone genus representing the Atelecyclidae in the fossil record is *Trichopeltarion*.

The ages and distribution of the fossil species are as follows: *Trichopeltarion decorus*, Miocene, Fiji; *Trichopeltarion huziokai*, Miocene, Japan; *Trichopeltarion inflatus*, Miocene, Japan; *Trichopeltarion greggi*, Miocene, New Zealand; *Trichopeltarion merrinae*, Miocene, New Zealand; *Trichopeltarion berglundorum*, Oligocene-Miocene, Washington State, U.S.A.; *Trichopeltarion granulosa*, Miocene, Washington State; and *Trichopeltarion n. sp.*, Miocene, Chile.

Phylogenetic analysis

Genera

A numerical cladistic analysis was conducted on all of the genera that have been assigned, at one time or another, to the family of Atelecyclidae in order to better understand the phylogeny of the group. They include *Bellia*, *Acanthocyclus*, *Corystoides*, and *Heterozius*, despite their recent removal to the Belliidae (Guinot, 1976). All of the genera with living representatives are included within the study, except *Corystoides*, for which a specimen could not be obtained or observed. Genera that are only represented in the fossil record, *Montezumella*, *Avitelmessus*, and *Cyclocancer*, were not used in the cladistic analysis because most defining characters are not preserved. Two of the genera within the study, *Thia* and *Kraussia*, have been placed in the Atelecyclidae as

Table 2. Characters and their states.

1. Front	8. antennule folding	15. lateral margins toothed
0: elongate bifid rostrum	0: fold longitudinally	0: singular teeth
1: complete, gently curved	1: fold transversely	1: lobes
2: two teeth	2: do not fold	2: compound teeth
3: tridentate	9. antennule size	3: compound and singular teeth
4: sulcate, gently curved	0: same size as antennae	4: none
5: curved, bilobed	1: larger than antennae	16. buccal region
6: complex biquad lobed	2: smaller than antennae	0: elongate
2. orbital direction	10. antennule cavity	1: strongly elongate
0: forward	0: tips fasten when folded	2: strongly quadrate
1: oblique	1: retract into cavity	3: quadrate
3. orbital construction	2: no cavity in use	17. anterior buccal limitation
0: series of spines or fissures	11. eye length	0: clear
1: complete	0: long, slender	1: unclear
4. antennae development	1: short, stout	2: moderate
0: well developed peduncle with flagellum	12. eye retraction	18. buccal frame
1: much reduced	0: retractable	0: third maxilliped within frame
5. antennae direction	1: nonretractable	1: third maxilliped overlapping frame
0: forward	13. canopy	19. sternal sutures
1: transverse	0: none	0: all incomplete
2: forward after 90° bend	1: canopy or spine protection	1: all complete
6. antennae folding	14. body shape	2: four and five incomplete
0: very flexible but not folding	0: pear shaped	3: four and five, five and six incomplete
1: folds upon itself	1: round	4: four and five, five and six, six and seven incomplete
2: nonfolding	2: strongly elongate oval	20. sternal shape
7. basal articles	3: strongly pentagonal	0: star
0: fixed, no projection	4: weakly pentagonal	1: elongate and narrow
1: fixed with projection in orbital hiatus	5: heart shaped	2: elongate and ovoid
2: movable	6: much wider than long	3: round
	7: weakly elongate oval	

members of the subfamily Thiinae Balss, 1957, but also have been recognized as belonging to a distinct family, the Thiidae, by Manning and Holthuis (1981). The genera *Telmessus* and *Erimacrus* have recently been placed within the Cheiragonidae by Števíč (1988); the family has since been expanded to include the fossil genus *Montezumella* by Schweitzer and Salva (2000). The remaining genera included in this cladistic study are currently considered to be in the Atelecyclidae: *Atelecyclus*, *Peltarion*, *Krunopeltarion*, *Trichopeltarion*, *Trachycarcinus*, *Pteropeltarion*, and *Phiosoma*. Although *Trachycarcinus* is here demonstrated to be the junior synonym of *Trichopeltarion* (see systematic paleontology), the two names have been retained as separate genera for the purposes of the cladistic analysis. The genus *Phiosoma* was used as the outgroup taxon because it is believed to be systematically distinct from the other genera. As will be demonstrated later, the genus has many characteristics assignable to the Majidae, and is thus considered to fall outside of the Atelecyclidae.

There are several synapomorphies that define monophyletic groups within the study. The reduced antennae is a synapomorphy that defines the monophyletic group known as the Belliidae (*Bellia*, *Acanthocyclus*, and *Heterozius*). Body shape is a character that has two states

which define monophyletic groups. A heart-shaped body is a synapomorphy that defines the Thiidae; (*Thia* and *Kraussia*). Incomplete sternal sutures four/five and five/six is a synapomorphy that defines the monophyletic group of the Cheiragonidae (*Telmessus* and *Erimacrus*), here shown as a crown group throughout the analysis. A pentagonal shape defines the monophyletic group known as the atelecyclids (*Atelecyclus*, *Pteropeltarion*, *Peltarion*, *Krunopeltarion*, *Trichopeltarion*, and *Trachycarcinus*). Although *Krunopeltarion* is identified as round it may still be considered as part of the monophyletic group. The round shape may be a more derived form of a pentagonal shape. The observation of a round shape of *Krunopeltarion* may be suspect as no entire specimen was observed; only the anterior half of a line drawing was seen. The lateral margins possessing compound teeth is a synapomorphy that defines the atelecyclids. *Pteropeltarion* lacks teeth due to being a much derived form of the group. The elongate ovoid sternal shape also defines the atelecyclids.

Characters and their states

The characters used within the analysis were chosen to characterize the taxa on a generic level (Figure 2,

Character	Minimum steps	Tree steps	Maximum steps	Consistency index	Homoplasy index	Retention index
1. front	6	8	8	0.750	0.250	0.000
2. orbital direction	1	1	2	1.000	0.000	1.000
3. orbital construction	1	3	3	0.333	0.667	0.000
4. antennae development	1	1	3	1.000	0.000	1.000
5. antennae folding	2	5	5	0.400	0.600	0.000
6. basal articles	2	2	3	1.000	0.000	1.000
7. antennule folding	2	3	5	0.333	0.333	0.667
8. antennule size	2	2	5	1.000	0.000	1.000
9. antennule cavity	2	2	3	1.000	0.000	1.000
10. eye length	1	2	5	0.500	0.500	0.750
11. canopy	1	2	4	0.500	0.500	0.667
12. body shape	7	7	10	1.000	0.000	1.000
13. lateral margins toothed	4	5	8	0.800	0.200	0.750
14. buccal region	1	2	2	0.500	0.500	0.000
15. anterior buccal limitation	2	3	5	0.667	0.333	0.667
16. buccal frame	1	3	5	0.333	0.667	0.500
17. sternal sutures	3	4	7	0.750	0.250	0.750
18. sternal shape	3	4	5	0.750	0.250	0.500

Figure 3. List of character states and the corresponding consistency index (CI), homoplasy index (HI), and retention index (RI) values for each.

Table 2). Several of the characters used in the analysis have been used by previous authors to define the family Atelecyclidae, and were discussed previously in this paper. These defining characters are: front morphology, orbital direction, orbital composition, antennae development, antennule folding, eye retraction, body shape, lateral margins with teeth, buccal frame elongate, and anterior buccal frame limitation. Additional characters used in here to define atelecyclid subfamilies include: basal antennal article mobility, use of antennule cavity, and development of orbital canopy. The remaining characters used in the analysis are believed to identify important systematic similarities and differences between the genera. These characters include: antennal direction, antennule size, eye length, third maxillipeds overlapping the buccal frame, sternal shape, and completeness of sternal sutures. The latter character was used by Guinot (1978) in subdividing her sections Podotremata, Heterotremata, and Thoracotremata, although no specific families were assigned. All of the possible states for each character are given in Table 2.

After a preliminary study using all previously used characters, only those deemed meaningful by PAUP were considered for analysis. Synapomorphies were discovered as discussed previously and these were used in establishing or upholding groups, that is families. Characters were chosen on the basis of being accessible and recognizable. Many characters employed by Guinot (1977, 1978) deal with the nature of the endophragmal skeleton, and were not used in this study.

Analysis

This analysis considers 14 genera listed in the previous section, and 20 characters. We conducted the cladistic analysis using PAUP 3.1.1 (Swofford, 1993) with data organized through MacClade 3.01 (Maddison and Maddison, 1992) and the search was performed using the branch and bound methods. Each method resulted in 294 most-parsimonious trees composed of 59 steps. All characters were unweighted and unordered so that the analysis included the fewest number of *a priori* decisions possible. The 294 most-parsimonious trees were generated with the majority of the 20 characters exhibiting some amount of homoplasy (Figure 3). A consensus tree was constructed that revealed a high degree of congruency (Figure 4). The consensus indicates how often a branching event occurs in a particular order and arrangement within a group of trees by displaying it in a percentage format on the most commonly used branching arrangement. Of the eight branching events calculated, one occurred 100 percent of the time, two occurred in the displayed fashion 84 percent of the time, one of the branching events occurred 69 percent of the time, and the others occur in the particular arrangement 51 to 54 percent of the time.

Major groupings of the genera

The 294 most-parsimonious trees revealed some major trends in grouping of the genera. The vast majority of those trees paired *Trachycarcinus* with *Trichopeltarion* and *Erimacrus* with *Telmessus* on discrete end-member branches. This signifies a very close phylogenetic relationship between each of these two pairs of genera, with *Erimacrus* and *Telmessus* possibly falling out as their own family, the

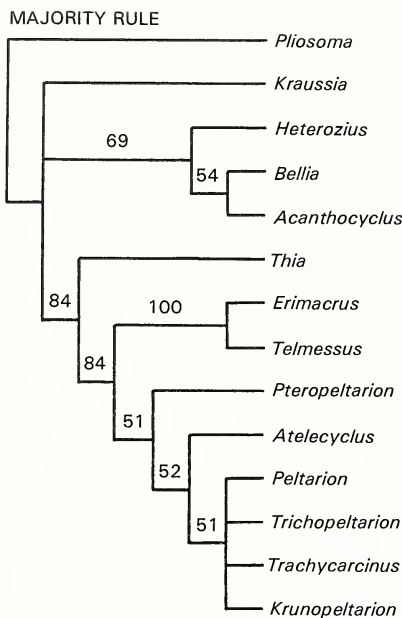


Figure 4. A consensus tree of the 294 most parsimonious trees. Rooted using the outgroup method.

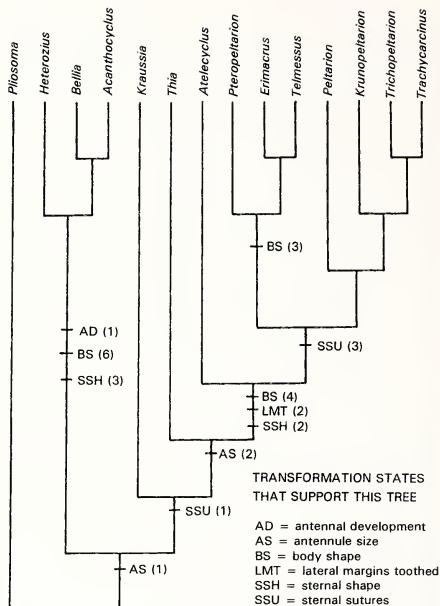


Figure 5. Of the 294 most parsimonious trees, this one is considered to best represent phylogenetic relationships between genera, and was used for character tracing.

Cheiragonidae. Within 154 of the 294 trees, *Peltarion* is bound within a distinguishable grouping along with *Krunopeltarion*, *Trachycarcinus* and *Trichopeltarion*. Other trends yielded information that support the removal of certain genera from the Atelecyclidae. *Heterozius*, *Bellia*, and *Acanthocyclus* were associated within a group distinguishable from the atelecyclids in 201 of the 294 trees, with *Bellia* and *Acanthocyclus* paired in a crown group 159 of the 201 times. The other 93 trees held these genera separate from the atelecyclid grouping, but arranged *Bellia*, *Acanthocyclus*, *Heterozius*, *Kraussia*, and *Thia* in a stepwise manner. Within 117 of the 294 trees showing groups other than the atelecyclids, *Kraussia* was associated with *Bellia*, *Acanthocyclus*, and *Heterozius* rather than with *Thia*. *Kraussia* and *Thia* never occurred as a pair on a terminal branchset, but did occur on adjacent branches within 182 of the 297 trees. The close association of *Kraussia* with the group known as the bellids, along with the lack of numerous groupings with *Thia* places the inclusion of *Kraussia* within the Thidae into question. Also, *Thia* does not appear to be closely related to the ingroup.

Character tracing

Since a detailed discussion of the phylogeny would not be relevant using the consensus tree, and 294 trees would produce a lengthy and at times contradictory description, one tree (Figure 5) that arranges the genera into meaningful groups was selected as most appropriately reflecting relationships; it will be discussed further. The tree has a consistency index (CI) of 0.712, a homoplasy index (HI) of 0.288, a retention index (RI) of 0.630, and a rescaled consistency index (RC) of 0.449.

Fronto-orbital region

The front has seven character states that define this tree, with only two of those appearing more than once. The most important state of frontal morphology from the standpoint of grouping genera was that of a tridentate front or rostrum. The grouping included *Trachycarcinus* and *Trichopeltarion* on a terminal branchset along with *Peltarion* and *Krunopeltarion*, whereas *Atelecyclus* was located on an adjacent branch. The only other state that occurred twice was that of having an elongate, bifid rostrum. *Pliosoma*, the outgroup, held this state, and it reoccurs

in *Pteropeltarion*. This character state is common for majids and explains the occurrence in *Pliosoma*. The observation that *Pteropeltarion* possesses a similar, but not identical rostrum, does not indicate a reappearance of the state phylogenetically within the group. The elongate bifid rostrum of *Pteropeltarion* is simply a unique front developed in one genus within the group.

The orbital direction has two states: 0, forward, and 1, oblique. All genera involved in this study with the exception of two have forwardly directed orbits. *Erimacrus* and *Telmessus* have obliquely directed orbits. This helps to define the closeness of their relationship, and places them on a terminal branchset which may be interpreted as the separate family Cheiragonidae. The forwardly directed orbit appears to be the norm and any deviation from it seems to unify the branching groups.

The construction of the orbit is reflected in two character states. State 0 defines an orbit comprised of a series of spines or nodes, while state 1 reflects a complete orbit. All of the genera that make up one of the major groups have an orbit that is complete, except *Bellia*, *Acanthocyclus*, *Heterozius*, and *Kraussia* are grouped on the basis of having a complete orbit, while *Bellia* is grouped along with them on the basis of other characters. The remaining genera could be said to be grouped based upon possession of an orbit made of a series of spines. This state, exhibited by *Thia*, draws *Thia* closer to the atelecyclid group and helps to disassociate it from *Kraussia*. From this it can be said that all atelecyclids possess an orbit comprised of a series of spines.

Antennae and antennules

The two states of antennal development are antennae with a well-developed peduncle and movable flagella (0) and antennae that are rudimentary, or much reduced (1). *Bellia*, *Acanthocyclus*, and *Heterozius*, thought to be bellids before the study was conducted, all have antennae that are much reduced. This is a very important character in separating the bellids from the atelecyclids (Figure 6). The character state of having antennae with well-developed peduncles and movable flagella is possessed by all of the other genera in this study. The true atelecyclids have well-developed antennae, as does *Pliosoma*, a majid. *Kraussia* possesses well-developed antennae which make it very different from the bellids with which it shows a close common ancestry. Based upon this character, *Bellia*, *Acanthocyclus*, and *Heterozius* are not considered to be atelecyclids, and *Kraussia* is not allied with the bellids.

The antennal direction is comprised of three states, antennae directed forward, antennae directed transversely, and antennae that are directed forward after a 90 degree bend. This character was interpreted as uninformative by MacClade due to the fact that only a single genus possessed state 2 and state 3 respectively. It is, however, noteworthy that it is *Heterozius*, which possesses state 2. This is another character by which *Heterozius* differs from the bellids to which it has been allied by previous authors. *Thia* exhibits state 3, and thus differs

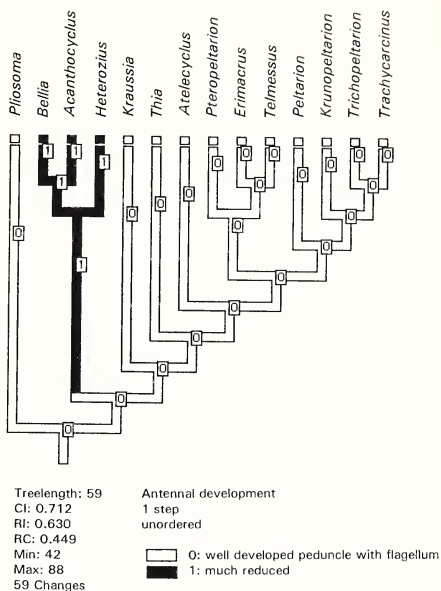


Figure 6. Tree showing antennal development. Genera with antennae that are reduced are shown to group together, suggesting possible phylogenetic relationships.

from the atelecyclids with which it was once classified. Whether this is grounds for removal of the *Thiinae* as a subfamily of the Atelecyclidae must await supportive evidence.

The folding of the antennae has three character states: a very well articulated and flexible antenna that does not completely fold upon itself, an antenna that does fold upon itself, and an antenna that does not fold and is not flexible. The two genera that possess antennae that fold upon themselves are *Heterozius* and *Thia*. This is not a sufficient basis to unite the two genera because they are very different in many other areas, but it does again indicate that they are different from all other genera in this study. *Bellia*, *Acanthocyclus*, *Kraussia*, *Trachycarcinus*, *Trichopeltarion*, *Pteropeltarion*, *Krinopeltarion*, *Telmessus*, and *Erimacrus* all have antennae that do not fold. This character therefore was not important in discerning groups, only in singling out those that do not belong to either the atelecyclids or bellids. *Peltarion* and *Atelecyclus* have the same state as the outgroup, antennae that do not fold but are extremely flexible. The well articulated and very flexible antennae possessed by these two genera may be a more advanced state than that of the

other genera in the atelecycloids, or it may be an observational error due to the preservation quality of the specimens. In any event, *Atelecycclus* and *Peltarion* resemble the outgroup more than either ingroup in this regard.

One character state of the basal antennal article is possession of an article that is fixed and has no projection filling the inner hiatus of the orbit (0). The second state is development of a fixed article that does have a projection filling the inner hiatus of the orbit (1). The third state (2) is possession of a movable basal antennal article with no projection. *Heterozius* is the only genus with a movable basal article. This is also a character that suggests that *Heterozius* might be very different from the rest of the genera in this study. There are two genera that have a basal article with a projection in the inner hiatus of the orbit. *Telmessus* and *Erimacrus* possess this character state, documenting their close relation within the cheiragonids. The state of having a fixed article with no projection does nothing in itself to discern groupings.

The nature of antennule folding is significant in defining the true atelecycloids. Antennules that fold longitudinally (0) are observed in all of the genera believed to be true atelecycloids and in the outgroup *Pliosoma*. The state of having antennules that do not fold (1) is held by *Bellia* and *Acanthocycclus*, and gives support to their being classified closely together. *Heterozius*, *Kraussia*, and *Thia* all possess antennules that fold obliquely (2). This state shows again that these genera may be very different from the atelecycloids and may indicate that *Thia* and *Kraussia* are related more closely than shown in the majority of the trees of this study.

Antennule size appears to group the genera in concordance with the tree chosen for discussion (Figure 7). The outgroup is the only genus with antennules the same size as the antennae (0). *Bellia*, *Acanthocycclus*, *Heterozius*, and *Kraussia* all have antennules that are larger than their antennae (1). While this serves to group them together on the tree, it should be noted that the antennules of *Kraussia* and *Heterozius* are not markedly larger than their antennae as they are in *Bellia* and *Acanthocycclus*. This may suggest that *Heterozius* and *Kraussia* are not as closely related to *Bellia* and *Acanthocycclus* as the tree might suggest. The other genera all have antennules that are much smaller than their antennae. This character state can be used to help define the true atelecycloids.

Possession and use of an antennule cavity is a function of not only the cavity itself, but also the antennule size. *Bellia* and *Acanthocycclus* are the two genera that do not possess a cavity (1) for their antennule, primarily because their antennules are very large. This state groups them even more closely together, while indicating that *Heterozius* and the other genera are different in this area. *Pliosoma*, having antennules whose tips fasten in the cavity, but are not completely housed by it, is the only genus with this character state (0). The other genera all possess a cavity that is functional (2).

Eye length is a character that can be quite variable when comparing groups on any level. The genera that possess

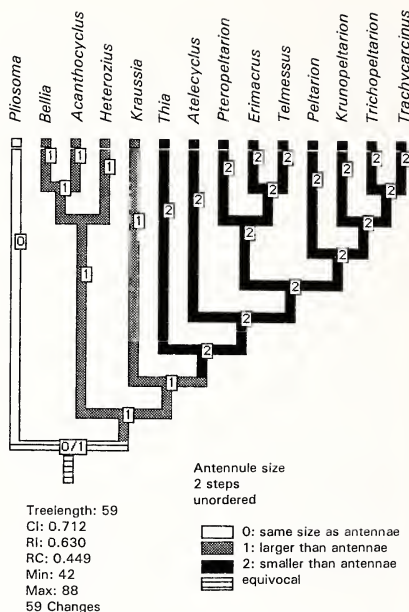


Figure 7. Antennule size observed as a character state within the tree. Those genera thought to be true atelecycloids possess antennules that are smaller than the antennae.

long slender peduncles appear to be closely related in more ways than eye length. This character may not be a strong choice for assigning relationships, but it does help support grouping of *Peltarion*, *Kranopeltarion*, *Trachycarcinus*, and *Trichopeltarion* established by other characters. All of the other genera seem to possess a type of short, stout peduncle.

The character of eye retractability was deemed uninformative because only one genus, *Bellia*, possessed eyes that could not be retracted into a cavity.

The character of eye protection has two states, that of having an eye that is not protected in any manner (0), and an eye that is protected by a canopy, series of spines, or calcification of the peduncle (1). In addition to the outgroup, the genera that have no eye protection were *Bellia*, *Acanthocycclus*, and *Kraussia*. This state could be interpreted either to group these three genera or merely indicate that they are different from the other genera. It did not serve as a very informative character.

Body shape and lateral teeth

Body shape is a character that is quite variable and useful in classification (Figure 8). *Pliosoma* is the only

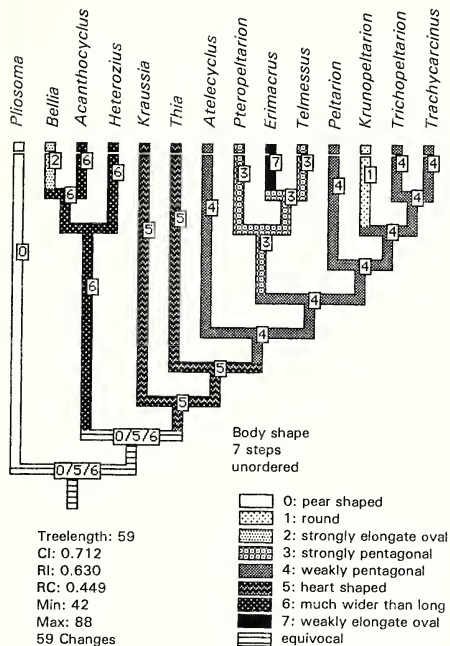


Figure 8. Character of body shape has many states. States and their generic relationships can be seen more clearly on the cladogram.

genus to possess the pear-shaped body (0) that is characteristic of the Majidae. The chordate, or heart-shaped, body (5) possessed by both *Thia* and *Kraussia* is important in the possible classification of the two genera. They are the only two genera that possess this unique outline. *Heterozius* and *Acanthocyclus* are different in many characters, but always seem to group closely together, and both have an outline that is much wider than long (6). While a pentagonal outline is a reoccurring shape within this group, there are variations upon it. Two genera, *Telmessus* and *Pteropeltarion*, appear to be strongly pentagonal (3). This is a strong reason why *Pteropeltarion* groups closely with *Telmessus* on several occasions. Exhibiting a weakly pentagonal outline with the anterior half of the carapace in some cases being almost circular (4) is a state held by four of the genera, *Trachycarcinus*, *Trichopeltarion*, *Peltarion*, and *Atelecyclus*. *Krunopeltarion* is considered to have a sub-circular shape (1) in this study. This state was assigned

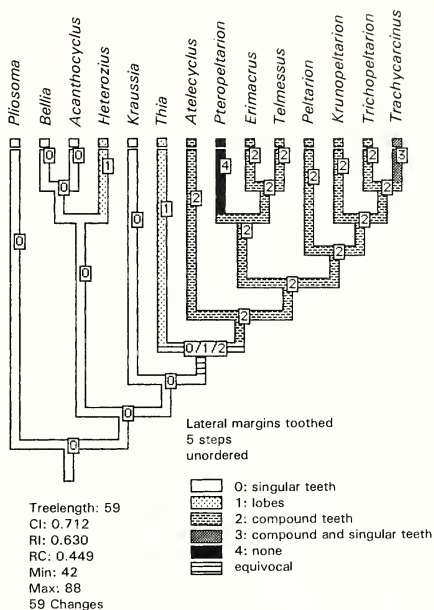


Figure 9. Characters of the lateral teeth. Lateral teeth is a character state that is observed in all genera believed to be true atelecyclids except for *Pteropeltarion*.

based upon the literature only (Števcíć, 1993). Observation of the carapace of *Krunopeltarion* could lead to the assignment of state 4, a weakly pentagonal outline. While *Erimacrus* is elongate ovoid in shape (2), it too appears to be somewhat pentagonal. It seems that the true atelecyclids may be described as having a weakly to strongly pentagonal carapace outline.

All of the genera in the study excluding one, *Pteropeltarion*, have some form of lateral teeth (Figure 9). *Erimacrus*, *Telmessus*, *Peltarion*, *Krunopeltarion*, *Trichopeltarion*, and *Atelecyclus* all possess compound teeth on the lateral margins (2). *Trachycarcinus* possesses teeth that are both compound and singular (3). This suggests that lack of teeth is a more advanced state in which case *Pteropeltarion* would be the most advanced genus among the atelecyclids. Both states three and four are autapomorphic and independently derived from state two. *Bellia*, *Acanthocyclus*, and *Kraussia* all have teeth that are singular (0). This suggests a reversal to the symplesiomorphic condition. *Heterozius* and *Thia* have lobes on their lateral margins (1). Again these states may either serve to rein-

force those groupings or only suggest that they are different from the grouping of *Erimacrus*, *Telmessus*, *Pteropeltarion*, *Trachycarcinus*, *Trichopeltarion*, *Atelecyclus*, *Krunopeltarion*, and *Peltarion*.

Buccal region

The possession of a quadrate buccal region has been considered to be a more advanced state of carcinisation by some authors (Guinot, 1976). Therefore, observing the degree to which the region appears quadrate may help to define groups and interpret phylogeny. Only *Acanthocyclus* and *Heterozius* have a buccal region that is quadrate, suggesting that they may be more advanced than the genera with elongate buccal regions.

The anterior limitation of the buccal frame, discrete (0) or covered by the third maxillipeds (1), is a character used in the study. There were no exact measurements taken; only general observations were made. It appears that *Kraussia*, *Heterozius*, and *Acanthocyclus*, along with the outgroup had clear limitations. This may help to unify the other genera into a group while keeping those with clear limitations separate. *Bellia* is the only genus with an unclear limitation that is not considered to be an atelecyclid. Based upon other, more strongly substantiated evidence, *Bellia* would not be grouped with the atelecyclids, but with those possessing clear anterior limitations.

The anterior limit of the buccal frame has two states. The maxillipeds fitting snugly into the frame provided is one state (0) that is possessed by *Pliosoma*, *Kraussia*, *Heterozius*, *Acanthocyclus*, *Bellia*, *Thia*, *Peltarion*, *Telmessus*, and *Erimacrus*. This state does not appear to be informative in defining the atelecyclids because not all genera presumed to be atelecyclids based upon this study possess the state, while others, not considered atelecyclids, do. However, the state of the third maxillipeds fitting incompletely, or overlying the frame (1), is possessed by five genera of the presumed atelecyclid group. This shows some relationship between these four genera, and again establishes *Trachycarcinus* and *Trichopeltarion* as being very closely related.

Sternum

The sternal sutures were characterized by five states (Figure 10). They involve the completeness of the sutures that lie between sternites four and five, five and six, six and seven, and seven and eight. The state of having all four sutures incomplete (0), which is considered the more derived state by some carcinologists, is exhibited by *Pliosoma*, *Heterozius*, and *Bellia*. The state of having all of the sutures complete (1), considered to be the most primitive state, is possessed by *Atelecyclus*, *Kraussia*, and *Thia*. This state indicates that a relationship between *Thia* and *Kraussia* might exist despite other differences. The only troubling indication of this character is that *Atelecyclus* and *Krunopeltarion* suture states differ from the rest of the presumed

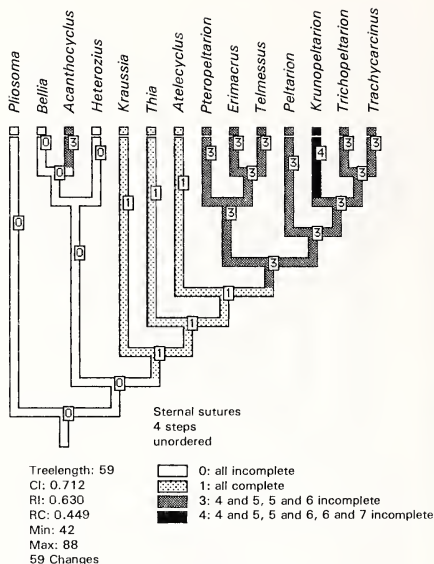


Figure 10. The character states of the sternal sutures represented on the cladogram.

atelecyclids. *Erimacrus*, *Telmessus*, *Pteropeltarion*, *Peltarion*, *Trichopeltarion*, and *Trachycarcinus* all possess the state of having sutures four/five and five/six incomplete. *Krunopeltarion* is the only genus within this study to have sutures four/five, five/six, and six/seven incomplete and seven/eight complete. One explanation for this would be that *Atelecyclus*, sharing the more primitive state with *Kraussia* and *Thia*, gave rise to the rest of the Atelecyclidae possessing the more derived suture patterns, with *Krunopeltarion* possessing the most derived suture pattern. This hypothesis needs the support of fossil evidence.

The sternal shape is thought to be important in establishing certain groups of genera, or families (Figure 11). *Kraussia* and *Thia* have elongate sterna that are almost identical in form. Based upon this character and that of body shape, it is evident why they have been classified so closely together in the past (Figure 12). *Pliosoma* has a unique sternum within the genera studied, but one that is typical of the Majidae. In this study the sternum of *Pliosoma* was simply described as star-shaped. *Bellia* and *Heterozius* have round sterna that either prove their relation to one another, or at least support their exclusion from the atelecyclids. The group considered to be the true Atelecyclidae, which consists of *Pteropeltarion*, *Peltarion*, *Krunopeltarion*, *Trachy-*

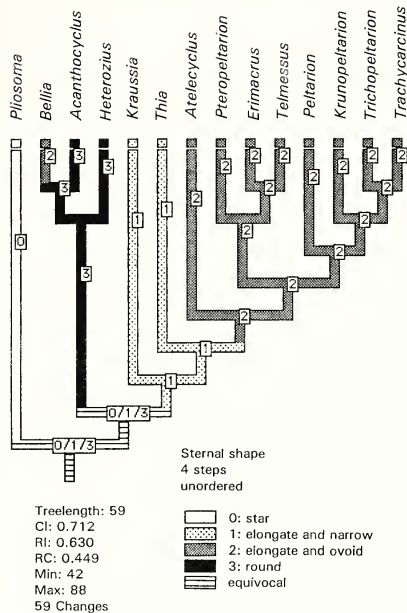


Figure 11. The character states of sternal shape represented on the cladogram.

carcinus, *Trichopeltarion*, and *Atelecyclus*, all have a sternum that is ovoid to elongate ovoid in outline. This is an important character possessed by all of the genera within that group, and helps to unify and classify them into the Atelecyclidae. This shape is shared with *Erimacrus* and *Telmessus*, but the sternum of these two cheiragonids is distinct in not covering the genital openings. The sternum actually is sculpted around the openings, a key character of the cheiragonids (Števíč, 1988; Schweitzer and Salva, 2000).

Results

Based upon this study, the genera examined fall within three clades. *Atelecyclus*, *Peltarion*, *Trichopeltarion*, *Trachycarcinus*, *Pteropeltarion*, and *Krunopeltarion* can be classified as the Atelecyclidae. These genera all have antennae with a well-developed and movable peduncle. The antennule size is much smaller than the antenna size in all of the genera. Antennules of the six aforementioned genera all fold longitudinally. The orbit is comprised of a series of spines and nodes, rather than being complete. Carapace shape is weakly to strongly pentagonal. The lat-

eral margins almost always bear teeth; the one exception being *Pteropeltarion*, which is considered to be a more derived form. The genera have sterna that are ovoid in shape, and all but *Atelecyclus* and *Krunopeltarion* have sternal sutures four/five and five/six incomplete. Sternal sutures four/five, five/six, six/seven, and seven/eight are all complete in *Atelecyclus*, suggesting that this is a more primitive suture state. *Krunopeltarion* has sutures four/five, five/six, six/seven incomplete, whereas seven/eight is complete, suggesting that this is a more derived suture state. The genera all have an elongate buccal region, with the anterior limitation of the third maxillipeds within the buccal frame being unclear to moderately unclear. These morphological similarities between the genera along with morphological differences with other genera within the study give support to the unity of family Atelecyclidae as defined.

While *Telmessus* and *Erimacrus* possess many characters in common with the atelecyclids, they have several characters that set them apart as their own separate family, the Cheiragonidae. This is reflected in the fact that they almost always group together as a crown group. This family is, however, very closely related to the atelecyclids.

The other genera studied have a less clear systematic placement. *Bellia*, *Acanthocyclus*, *Corystoides*, and *Heterozius* remain in the family Belliidae as established by Guinot (1976) (Figure 13). Although the defining characters of the belliids are unclear, the four genera all possess antennae that are much reduced and are smaller than their antennules. Other than these two characters, the genera lack common character states used in this study. The carapace shape, sternal shape, and sternal sutures are different among the four genera, making their true phylogeny unclear. *Heterozius*, by far, has the largest number of morphological differences among these four genera, making placement in this family questionable. Although there must be more research regarding the systematic placement of *Heterozius*, it is not within the scope of this work. However, *Heterozius* may belong with the xanthids, an assignment supported by several previous authors (Richardson, 1949).

The classification of *Thia* and *Kraussia* is brought into question based upon results of this study. The two genera exhibit some morphological differences; but for the moment, their close relationship was upheld. The heart-shaped carapace, elongate sternum, complete sternal sutures, elongate buccal region, and transversely folded antennules give support to their relationship. The genera should not be placed as a subfamily of the Atelecyclidae, but should be referred to the distinct family Thiidae. Differences of carapace and sternal shape, transversely folding antennules, and complete sternal sutures suggests that these genera may be more primitive than the Atelecyclidae. Similarities between *Atelecyclus* and the Thiidae may suggest that the Thiidae are ancestral to the Atelecyclidae. Much more evidence would be needed to support this suggestion.

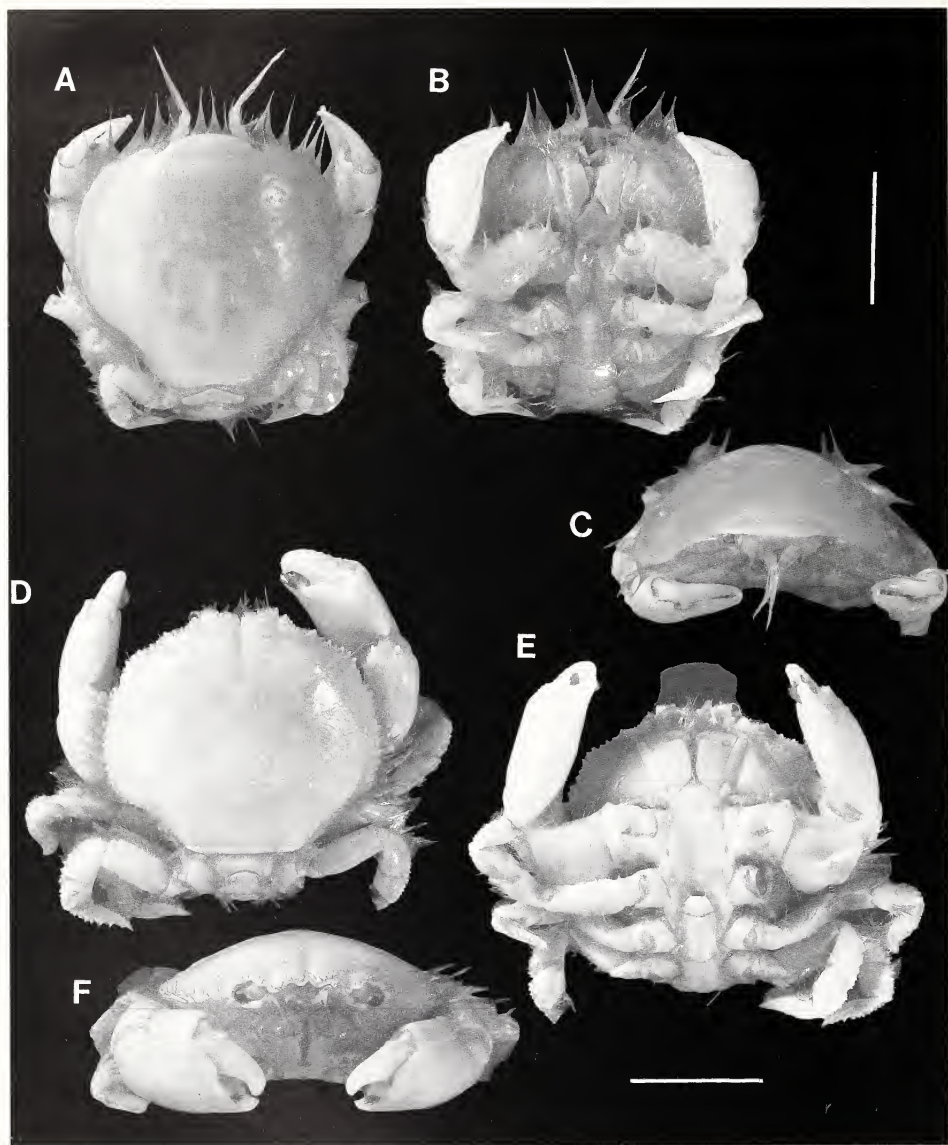


Figure 12. Thiidae. Dorsal (A), ventral (B), and orbital (C) views of *Thia scutella*, USNM 264628; dorsal (D), ventral (E), and orbital (F) views of *Kraussia hendersoni*, USNM 23157. Scale bars equal 1 cm.

List of Museum and Specimen Acronyms

- AD = Specimens belonging to Ann DeBode of Lyttleton, New Zealand. (A private collection.)
- AR = The Institute of Geological and Nuclear Sciences Limited, Lower Hutt, New Zealand.
- BNMH = The Natural History Museum, London, England.
- CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
- Cr. = The National Museum of New Zealand, Wellington.
- DM = Specimens belonging to Don McLauchlan of Christchurch, New Zealand. (A private collection.)
- IGPS = Institute of Geology and Paleontology, Sendai, Japan.
- MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
- MNHN = Muséum National d'Histoire Naturelle, Paris, France.
- NMNZ = The National Museum of New Zealand, Wellington.
- P = Australian Museum, Sydney, Australia.
- USNM = The U. S. National Museum of Natural History, Washington, DC
- zfc = The Canterbury Museum, North Canterbury, New Zealand.

Systematic Paleontology

Order DECAPODA Latreille, 1803
 Infraorder BRACHYURA Latreille, 1803
 Section HETEROTREMATA Guinot, 1977
 Family ATELECYCLIDAE Ortmann, 1893

Diagnosis

Antennules fold lengthwise into a cavity, and are smaller than antennae. Movable part of antenna well developed but does not fold upon itself. Antennae usually hairy. Basal antennal article fixed. Orbits constructed of a series of spines. Lateral margins with teeth that are mostly compound. Carapace never very broad, but subcircular, elongate-suboval, strongly pentagonal, or weakly pentagonal with the anterior subcircular. Buccal region elongate. Sternum elongate ovoid with transverse sutures *four/five* and *five/six* being incomplete, all four sutures, (*four/five*, *five/six*, *six/seven*, and *seven/eight*) being complete, or sutures *four/five*, *five/six*, and *six/seven* incomplete with *seven/eight* complete.

Remarks

The following genera are retained in the family Atelecyclidae based upon the diagnostic characters:

Atelecyclus, *Peltarion*, *Trichopeltarion*, *Trachycarcinus*, *Pteropeltarion*, and *Krimopeltarion*.

Erimacrus and *Telmessus* should remain in the Cheiragonidae as defined by Štević (1988) and updated by Schweitzer and Salva (2000). The key characteristics of the family are discussed below. Characteristics observable in the fossil record include: Front bilobed or quadlobed with axial notch. Basal antennal article with triangular projection extending into orbital hiatus. Complex female genital opening not covered by abdomen. Orbits possessing both inner and outer orbital spines and median fissure or notch. Dorsal carapace as wide as long or slightly longer than wide; spined frontal and orbital margins; lateral margins with six or seven teeth in extant genera; posterior quarter of dorsal carapace typically rectangular; posterior margin possessing a broad central cavity. Carpus characterized by spinose outer margin with spines sometimes arranged in rows. Mani of first pereopods ornamented with small spines on the outer margin. For more details see Schweitzer and Salva (2000). In addition, the larvae are similar to each other and distinct from larvae of all other brachyuran families (Rice, 1980).

Bellia, *Corystoides*, *Acanthocyclus*, and *Heterozius* have been placed within a separate family, Belliidae (Guinot, 1976). They are distinct from the atelecyclids in that their antennae are much reduced, the antennules are larger than the antennae and do not fold, or fold transversely. The lateral margins have no compound teeth. While the aforementioned characters are the only ones for which all of the Belliidae differ from the Atelecyclidae, individual genera of the Belliidae possess other characters distinctly different from those possessed by any of the atelecyclids.

Bellia exhibits several characters that are congruent with atelecyclid characters. The tridentate front, orbit formed of a series of spines, elongate ovoid carapace shape, elongate buccal region, and ovoid sternal outline ally *Bellia* with the atelecyclids. However, the nature of the antennae and antennules, and the incomplete sternal sutures indicate that it is sufficiently different from atelecyclids to warrant placement in a separate family.

In addition to the diagnostic belliid characters, *Acanthocyclus* differs from the atelecyclids by having a front that is gently curved and bilobed and a body that is much wider than long. The orbit is complete rather than comprised of a series of spines. The buccal region is quadrate with the anterior limitation of the third maxilliped appearing distinct, and resting entirely within the frame. The shape of the sternum is round.

Heterozius possesses characters that are not only distinct from the atelecyclids, but also from the other bellids. *Heterozius* has a unique, gently curved, and sulcate front. The antennae fold upon themselves, a characteristic possessed by neither typical atelecyclids nor other bellids. This genus is distinctly different from the other genera of the two families in question in exhibiting a movable basal antennal article, and in having antennules that fold transversely. Characters distinguishing *Heterozius* from the atelecyclids

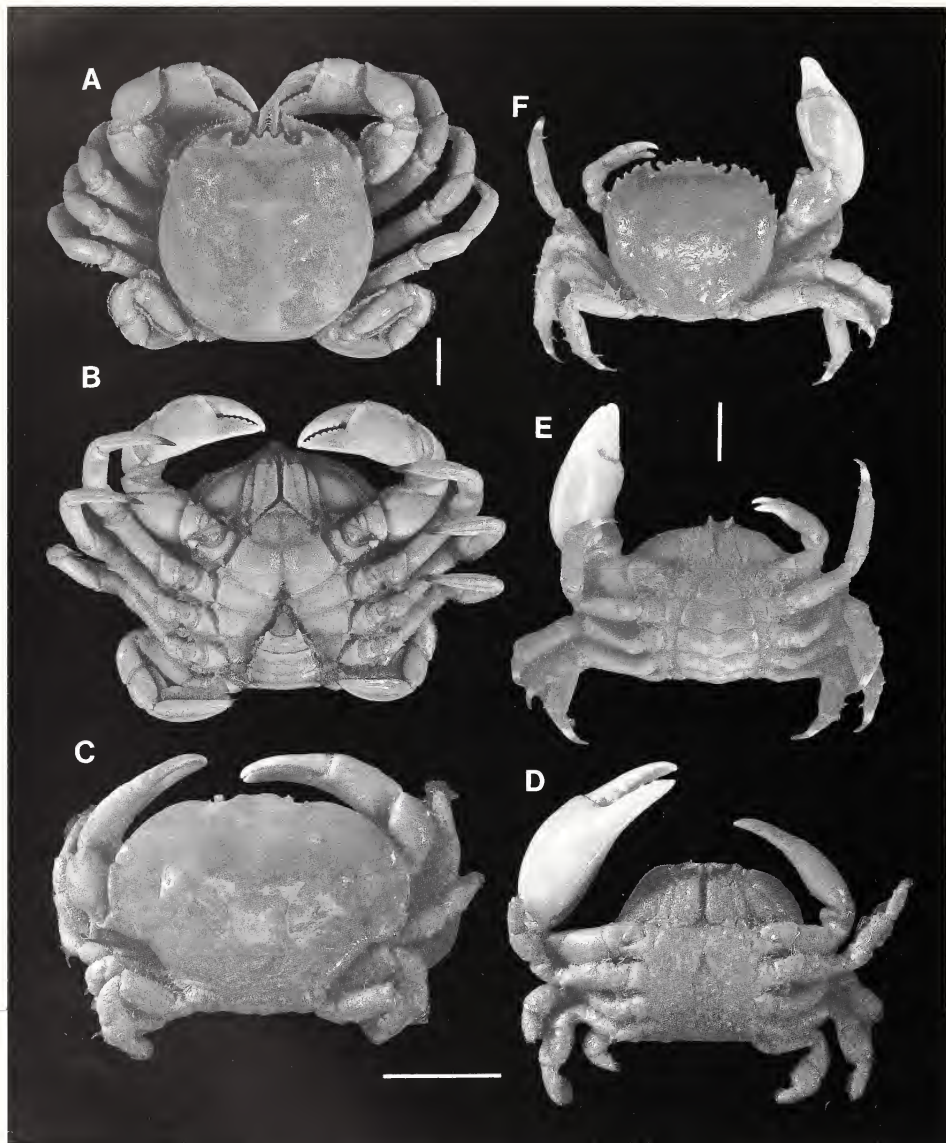


Figure 13. Belliidae. Dorsal (A) and ventral (B) views of *Bellia picta*, USNM 22066. Dorsal (C) and ventral (D) views of *Heterozoeus rotundifrons* USNM 18163; ventral (E) and dorsal (F) views of *Acanthocyclus albatrossi*, USNM 156528. Scale bars equal 1 cm.

but allying it to some belliiids are development of a complete orbit, a carapace which is much wider than long, a quadrate buccal region with the anterior limitation of the third maxilliped clear and within the frame, a round sternum, and four incomplete sternal sutures. While *Heterozius* is clearly not an atelecyclid, the differences between *Heterozius* and the other belliiids put its placement within the Belliidae into question.

While Guinot (1976) believed that the four genera should be, in reference to the Balss (1957) classification, placed in the family Belliidae and assigned to superfamily Bellioidea, no diagnostic characters were established for the family.

The genera *Bellia*, *Corystoides*, and *Acanthocyclus* have numerous morphological similarities, especially the nature of the frontal region including antennae and antennules. These characters form the definitional bases for the family. *Heterozius* on the other hand, is markedly different from these three genera, including *Acanthocyclus*, which superficially appears similar to *Heterozius*. The lack of morphological similarities with authentic belliiids, along with the fact that it is a genus endemic to New Zealand, supports placement of *Heterozius* in its own group or in the Xanthidae to which it was previously assigned. It is clearly evident that *Heterozius* is neither an atelecyclid nor a belliid.

Thia and *Kraussia* were first classified in association with the atelecyclids in the subfamily Thiinae, which was within the Cancridae, by Alcock (1899). Atelecyclinae was also a subfamily of the Cancridae. Authors as recent as Balss (1957) and Sakai (1976) have elected to retain the Thiinae as a subfamily of the Atelecyclidae. The present work demonstrates that gross morphological differences of the carapace outline, ornamentation, front, lateral margin teeth, sternum, and nature of sternal sutures warrants placement of *Thia* and *Kraussia* in a distinct family, Thiidae.

Kraussia has almost always been classified with *Thia* in the Thiidae or in the subfamily Thiinae within the Atelecyclidae. Their heart-shaped carapaces with poorly defined regions is the most obvious basis for their classification together. They both possess antennules that fold transversely and that are retracted into a cavity. The basal antennal articles are fixed in both genera. Each has the third maxilliped covering the mouth and fitting snugly into the elongate buccal frame. The two genera have sterna that are elongate and similar in shape. The four transverse sutures of the sternum are incomplete in both genera. While these common characters may help to unite these two genera, there were enough differences between the genera to separate them in the cladistic analysis.

The fronts of *Thia* and *Kraussia* are different. *Thia* has a complete and gently curved front, while *Kraussia* has a front that is comprised of a complex series of four lobes bearing teeth. The orbit of *Thia* is made of a series of spines or nodes, while *Kraussia* has a complete orbit. *Thia* possesses antennae that are directed forward only after a unique 90 degree bend, and *Kraussia* has antennae that are non-folding and directed forward. *Thia* possesses antennules that are smaller than their

antennae, but *Kraussia* possesses antennules that are larger than their antennae. Thus, the nature of the carapace and sternum unify these two genera, while the nature of the antennules and antennae serve to keep them separate. The nature of the antennae and antennules is very important in distinguishing the Atelecyclidae from the Belliidae at the generic level. It is unwarranted, however, to assign *Thia* and *Kraussia* to separate families. The similarities identified constitute a basis for retaining *Kraussia* within the Thiidae.

The monospecific genus *Phiosoma* Stimpson which was established for *Phiosoma pavifrons* Stimpson should be assigned to the Majidae. *Phiosoma* was classified with the atelecyclids based upon the broad diagnosis of the family. This placement was upheld by Rathbun (1930b) and has been reviewed by Guinot (1979, p. 12) who classified *P. pavifrons* within the Majidae based upon the nature of the second male pleopod which is very short in majids and long in the atelecyclids. The nature and shape of the thoracic sternum is characteristic of majids (Figure 14). This is true not only in shape, but also with regard to the fusion of transverse sutures four/five, five/six, six/seven, and seven/eight. The zone of fusion at the termination of sutures six/seven and seven/eight in the median region is similar to that of other majids. The first male pleopod is like that of majids in shape and style. Other general characteristics of the Majidae that *Phiosoma* possesses include the pear-shaped body, orbits comprised of a complex series of spines, and long slender walking legs. The present work supports Guinot (1979) in placing *Phiosoma* within the Majidae, with Pisinae as the appropriate subfamily.

Genus *TRICHOPELTARION* A. Milne Edwards, 1880

Type species

Trichopeltarion nobile A. Milne Edwards, 1880.

Diagnosis

Carapace pentagonal, weakly pentagonal, or subcircular; slightly longer than broad or nearly as long as broad excluding lateral spines; strongly convex. Carapace ornamented with granules, tubercles, or a combination of the two. Granules or tubercles may clump and define regions, or crest swollen areas that define regions. Degree of ornamentation fluctuates, larger specimens may be more sparsely adorned. Front prominent, not very broad, with three sharp teeth or spines. Central spine of three frontal spines may be shorter, longer, or of equal length. Orbits directed forward, defined by spines separated by wide gaps, two hiatuses above, one below, and one at inner angle, lower wall formed by carapace with extending sub-orbital spine; supraorbital spine compound, rectangular, crested by spinelets or bars; inner suborbital angle spiniform. Anterolateral margins with compound teeth or cylindrical spines, which may have tiny spinelets toward base.



Figure 14. *Pliosoma pavifrons*, dorsal (A), orbital (B), and ventral (C) views of USNM 77851. Scale bar equals 1 cm.

Intersection of anterolateral and posterolateral margins bears lateral spine or tooth. Spine varies from small, compound, with triangular outline, to long, cylindrical, possibly bearing spinelets. Eye stalks slender, retractile within orbits. Antennules fold longitudinally. Basal article of antenna lies imperfectly within inner hiatus of orbit, short, subcylindrical, armed to unarmed, imperfectly fused to carapace; second article longer and more slender than first, third about equal to second in length but more slender; flagellum coarse, stout, setose; antennae less than half as long as carapace. Epistome fairly well defined, sunken, overlapped by external maxillipeds. Buccal orifice square-cut, longer than broad, anterior margin not well defined, not completely covered by outer maxillipeds, which are somewhat elongate with merus narrower than ischium. Ischium of third maxillipeds produced at anterointernal angle; merus rounded at anteroexternal angle, obliquely truncated at anterointernal angle. Sternum an elongate oval, widest at intersection of fourth and fifth sternites. Sternites one-three with a sagittate tip, lies between bases of third maxillipeds and anterior limit of coxae of first pleopod, measures one-fourth of total sternum length. Fourth sternite greatly curved around coxae of first pleopods, fused with three. Chelipeds massive and unequal in mature males. Legs stout, of moderate length, may be hairy especially along margin, may have spines or granules along margins, ending in slender, straight, styli-form dactyli.

Included species

Trichopeltarion nobile A. Milne Edwards, 1880, p. 20; *Trachycarcinus corallinus* Faxon, 1893; *Trichopeltarion ovale* Anderson, 1896, p. 103; *Trachycarcinus glaucus* Alcock and Anderson, 1899, p. 9; *Trachycarcinus alcocki* Doflein, 1903; *Trachycarcinus balssi* Rathbun, 1932, p. 36; *Trachycarcinus sagamiensis* Rathbun, 1932, p. 36; *Trachycarcinus decorus* Rathbun, 1945, p. 377; *Trachycarcinus huziokai* Imaizumi, 1951, p. 33; *Trichopeltarion fantasticum* Richardson and Dell, 1964, p. 148–151; *Trichopeltarion wardi* Dell, 1968, p. 275–276; *Trichopeltarion greggi* Dell, 1969, p. 367–371; *Trachycarcinus elegans* Guinot and Sakai, 1970, p. 201; *Trachycarcinus intensi* Crosnier, 1981, p. 303; *Trachycarcinus crosneri* Guinot, 1986, p. 807; *Trachycarcinus moosai* Guinot, 1989, p. 361; *Trachycarcinus inflatus* Kato, 1996, p. 515; *Trichopeltarion berglundorum* Schweitzer and Feldmann, 1999, p. 237–242; *Trichopeltarion granulosa* Schweitzer and Salva, 2000, p. 291–294; *Trichopeltarion merrinae* Schweitzer and Salva, 2000, p. 294–296. *Trachycarcinus intensi* was never directly observed and no photographic illustrations studied. While the species probably is a member of *Trichopeltarion*, observation of only one line drawing leaves room for question.

Excluded species

The following species previously classified as *Trachycarcinus* cannot be embraced within the new and expanded definition of *Trichopeltarion*: *Trachycarcinus lystricosus* Garth in Garth and Haig, 1971, p. 6.3; *Trachycarcinus delli* Guinot, 1989, p. 365; and *Trachycarcinus foresti* Guinot, 1989, p. 369. They should be reclassified into another already existing, or a new, genus. Conclusions were made based on one line drawing of *Trachycarcinus lystricosus*; direct observation of specimens or figures would reinforce the exclusion of the species from *Trichopeltarion*.

Remarks

The differences between specimens of *Trachycarcinus* and *Trichopeltarion* with regard to shape, degree of ornamentation, nature of the front, nature of the anterolateral spines, and the nature of the lateral spines are all at the species level. Because the aforementioned characters display such a wide range of variation, observed in several states within each genus, the generic definitions overlap. Based on observations of some 200 specimens, these species possess enough common generic characters to warrant synonymizing *Trachycarcinus* with *Trichopeltarion*.

Previous authors have drawn attention to the similarities between the two genera, and have failed to identify diagnostic differences. Attempts to differentiate between the genera of *Trichopeltarion* A. Milne Edwards, *Trachycarcinus* Faxon, and *Peltarion* Jaquinot by Rathbun (1930b, p. 149) seem rather arbitrary. In the description of a new species of *Trichopeltarion*, Dell (1969, p. 370) indicated his preference for uniting *Trachycarcinus* with *Trichopeltarion* based upon the arbitrariness of differentiating characters. The degree of tuberculation on the margin and the length of the lateral spines are only differences of degree (Richardson and Dell, 1964, p. 146). Since that time Pequegnat (1970, p. 187) synonymized *Trachycarcinus spinulifer* with *Trichopeltarion nobile* for reasons discussed below, while Guinot (1989, p. 355) placed *Trichopeltarion ovale* in *Trachycarcinus*. The problem of assigning species to a particular genus when the type descriptions are so similar continues to plague authors. The nature of the problem cannot be addressed simply by observing each species and assigning it to the genus to which it is most similar, based upon reference to the respective type species, *Trichopeltarion nobile* and *Trachycarcinus corallinus* (Faxon, 1893). Since so many of the species exhibit characters that are found in both type species, it is likely that there is merely a wide range of variation within one genus.

There has been much attention given to the carapace outline or shape when differentiating between *Trichopeltarion* and *Trachycarcinus*. *Trachycarcinus* has been considered to be pentagonal in outline with long, nearly straight anterolateral margins (Rathbun, 1930b), while *Trichopeltarion* has been described as having a subcircular to oval outline. It does appear that the type species of each genus exhibits

Table 3. Principal diagnostic characters of *Trachycarcinus* and *Trichopeltarion* cited in the literature compared to observed characters.

Characters	Ideal for <i>Trachycarcinus</i>	Ideal for <i>Trichopeltarion</i>	Observed for <i>Trachycarcinus</i>	Observed for <i>Trichopeltarion</i>
outline/shape of carapace	pentagonal ¹	subcircular ¹ to orbicular	<i>T. balssi</i> is subcircular	<i>T. fantasticum</i> juveniles are pentagonal
ornamentation density of carapace	tubercles on entire carapace ²	smooth with small granules near margins ¹	tubercles on entire carapace	tubercles on entire carapace, <i>T. nobile</i> smooth posteriorly
lateral spines	?	long ²	long cylindrical to short and triangular	long cylindrical to short and triangular
ornamentation type/style	tubercles, no hairs ²	fine granules, short sparse fine hairs ¹ frosted tubercles	granules to tubercles, short hairs on some	granules to tubercles, short hairs on most
lateral margins (anterolateral)	toothed ³	armed with spines ²	cylindrical spines or triangular compound teeth	cylindrical spines or triangular compound teeth

¹Rathbun, 1930b²Richardson and Dell, 1964³Sakai, 1976

these outlines: *Trichopeltation nobile* is subcircular and *Trichopeltarion corallinus* is pentagonal. However, when all species are observed, the types seem to have the most extreme outlines of either case. Several species, formerly referred to *Trachycarcinus* are as circular, or even more circular, in outline than species of *Trichopeltarion*. Likewise, all species of *Trichopeltarion* have a pentagonal nature. It is the shape or outline of the anterolateral margin that gives the carapace the appearance of being subcircular. When the anterolateral margins are slightly rounded as in *T. nobile*, *Trichopeltarion greggi*, *Trichopeltarion fantasticum*, *Trichopeltarion wardi*, *Trichopeltarion ovalis* (Anderson, 1896), *Trichopeltarion balssi* (Rathbun, 1932), *Trichopeltarion crosneri* (Guinot, 1986), *Trichopeltarion alcocki* (Doflein, 1903), and *Trichopeltarion intensi* (Crosnier, 1981), the carapace has an outline that is more subcircular than pentagonal. If the anterolateral margin is not gently curved, but extends in a straight line from the base of the frontal spines to the base of the lateral spine, then the carapace outline has a more pentagonal appearance as in *T. corallinus*, *Trichopeltarion elegans* (Guinot and Sakai, 1970), *Trichopeltarion glaucus* (Alcock and Anderson, 1899), *Trichopeltarion moosai* (Guinot, 1989), *Trichopeltarion sagamiensis* (Rathbun, 1932), and some *Trichopeltarion crosneri*. The majority of the species have a posterolateral margin that is similar in outline, convex and gently curving. A small number of the species have a pos-

terolateral margin that is nearly straight and not as convex as the margin of *T. nobile*. The straight posterolateral margin results in an even more pronounced pentagonal outline in *T. elegans*, *T. glaucus*, and *T. moosai*.

All of the known species of *Trichopeltarion* possess a lateral spine. The lateral spine is usually prominent. In some species it may not be much larger or longer than the anterolateral spines. The spines have two forms: long and cylindrical, or more compact and triangular with a possible cylindrical spine extending from the apex. Both forms of the lateral spine may possess tiny spinelets. There is a certain amount of variability in density and number of spinelets, but all species within the group exhibit one variation of the two forms.

All species within *Trichopeltarion* and species previously referred to *Trachycarcinus* have a tridentate rostrum. The length of the spines relative to one another varies, as does the amount of protrusion of the rostrum. All species also have a somewhat rectangular inner orbital spine crested with small teeth or spinelets. The orbit bears two hiatuses above, one between the inner orbital spine and the supraorbital spine, the other between the supraorbital spine and the outer orbital spine. The anterolateral margin is adorned with spines that can be compound, or of a singular, more cylindrical nature. *Trichopeltarion nobile*, *T. fantasticum*, *T. wardi*, *T. greggi*, *T. crosneri*, *T. balssi*, *T. elegans*, *T. glaucus*, and *T. intensi* all have anterolateral spines that are compound and somewhat triangular in shape. Some have sharp

spinelets making the spines compound, while others have more rounded tuberclelike spinelets on the anterolateral spines. *Trichopeltarion alcocki* and *T. moosai* have compound spines that are longer, more cylindrical, and more strongly curved anteriorly than other species of *Trichopeltarion*. They also possess such small spinelets that they appear almost singular. *Trichopeltarion ovalis* has anterolateral spines that are very sharp, and although they are compound they do not closely resemble those of any of the other species. They are a series of sharp spines, not long as in *T. alcocki*, and not triangular as in *T. wardi*.

From the study of this wide range of specimens assigned to one of the two genera, *Trachycarcinus* and *Trichopeltarion*, it can be seen that several of the characteristics previously used to differentiate the genera actually overlap between the two genera. The possession of characters previously described as belonging to *Trichopeltarion* by species assigned to *Trachycarcinus*, and characters previously described as belonging to *Trachycarcinus* by species traditionally referred to *Trichopeltarion*, along with the common morphologic criteria, to be discussed below, are the basis for considering the genera synonymous (Table 3).

All of the species now embraced within *Trichopeltarion* have well to moderately well defined regions marked by one of the following ornamentation types: tubercles that are clumped more tightly in regions that appear swollen (*T. wardi* and *T. crosneri*), swollen pustulose areas that may be crested by granules or tubercles (*T. fantasticum* and *T. nobile*), or clumping of tubercles that are themselves crested by granules (*T. ovalis*). These tubercles may form patterns within the regions and the patterns may be common within the genus, or may be species specific.

The antennae are similar across all the species. The basal article is subcylindrical and somewhat flattened. Although not completely closing off the inner hiatus of the orbit, it does appear to rest above or adjacent to the suborbital spine imperfectly filling the void. The basal article is unarmed except in the case of *T. glaucus* and possibly *T. elegans*. This slightly enlarged basal article is imperfectly fused to the carapace. The second article is longer and more slender than the basal article, the third about equal in length to the second but more slender; all are furnished with setae. The antennae appear to be somewhat fragile and are longer than half the carapace length only in two species previously assigned to *Trachycarcinus*. The two species *T. delli* and *T. foresti* cannot be included within the genus *Trichopeltarion* due to the very long and stout nature of their antennae. While these species are closely related to the genus, they possess enough differentiating characters that make their assignment to a separate, not yet established, genus the most reasonable alternative.

As mentioned above, the structure of the orbit is the same throughout the genus. The orbits are directed forward and are imperfect. There are two hiatuses above, one

Table 4. Measurements (in mm) taken on specimens of *Trichopeltarion greggi*, *Trichopeltarion fantasticum*, and *Trichopeltarion nobile*. Carapace lengths are measured excluding the frontal spines, and chela lengths are measured from carpal articulation to tip of movable finger. Measurement of np denotes that the feature was not present, or not preserved.

Species	Specimen	Carapace length	Chela length	
			rt.	lt.
<i>T. greggi</i>	DM 59	69.39	87.88	24.84
	DM 49	63.82	65.97	np
	zfc 178	83.79	83.80	np
<i>T. fantasticum</i>	NMNZ	49.73	50.00	19.64a
	NMNZ	69.00?	96.00?	30.00?
<i>T. nobile</i>	USNM 128427	72.36	113.89	44.44
	USNM 93674	73.96	31.77	99.48

below, and one at the inner angle. The lower wall is formed by the carapace and an extending suborbital spine.

The buccal frame is elongate and rectangular in all species of *Trichopeltarion*. The anterior margin of the buccal frame is not distinctly defined. The third, or outer, maxillipeds are elongate, similar in morphology, and fit into the frame in the same manner. The ischium of the third maxilliped is produced at the anterointerior angle. The merus is rounded at the anteroexternal angle, and is obliquely truncated without emargination at the anterointernal angle. The exopod parallels the merus, and is not obliquely truncated adjacent to it.

The sternum has the same shape, outline, and degree of fusion of sutures throughout the genus. Each of the first three plates, or sternites, is fused into a sagittate tip that rests between the bases of the third maxillipeds and the anterior limit of the coxa of the first pleopod. The fusion of sternites one through three measures approximately one-fourth of the total sternal length, with the fourth sternite also fused with the first three and possessing a strongly concave lateral margin. Sternites five and six are gently convex on the lateral margins with a straight anterior margin extending posteriorly adaxial. Sternites five and six mark the widest portion of the overall ovoid sternum. The fifth overlies the fourth, the sixth overlies the fifth, and the seventh overlies the sixth. The seventh sternite is gently convex on the lateral margin, and curves adaxially towards the posterior, resulting in a decrease in width posteriorly. The eighth sternite is very small and is shaped in a manner that completes the ovoid outline of the sternum.

The legs on all species are similar in form, moderately long, and may possess hairs of variable length, especially on the margins. Many of the legs possess some type of granules, tubercles, or even sharp spines. The dactyli are styliform, straight, and slender.

Many of the species possess an enormous major chela in the mature males. The males do not all have major chelae, and possession of a major chela is not necessarily size relat-

Table 5. Measurements (in mm) of *Trichopeltarion* taken from adult representatives. The length measures from the front, excluding the frontal spines, to the posterior margin. Width measures exclude the lateral spines.

Species	Museum no.	Length	Width
<i>Trichopeltarion nobile</i>	USNM 128427	72.36	70.42
<i>Trichopeltarion corallinus</i>	USNM 20618	27.50	30.40
<i>Trichopeltarion ovale</i>	USNM no no.	44.07	40.13
<i>Trichopeltarion glaucus</i>	BNMH syntype	13.64	12.35
<i>Trichopeltarion alcocki</i>	MNHN B11571	70.14	62.03
<i>Trichopeltarion balssi</i>	USNM 65058	19.78	18.32
<i>Trichopeltarion sagamiensis</i>	type, Balss 1922	29.46	28.92
<i>Trichopeltarion decorus</i>	USNM 498414	14.30	16.70
<i>Trichopeltarion huziokai</i>	IGPS 73235	30.00	22.00
<i>Trichopeltarion fantasticum</i>	Cr. 6566	49.24	45.76
<i>Trichopeltarion wardi</i>	P 14789 holotype	23.94	20.12
<i>Trichopeltarion greggi</i>	zfc 52	69.92	63.72
<i>Trichopeltarion elegans</i>	holotype	24.82	24.25
<i>Trichopeltarion crosneri</i>	MNHN B12689	49.55	43.27
<i>Trichopeltarion moosai</i>	MNHN B11570	13.24	11.82
<i>Trichopeltarion berglundorum</i>	CM 39667	18.63	19.12
<i>Trichopeltarion inflatus</i>	IGPS 102782	30.30	26.70

ed within the genus, but is age related within each species. Pequegnat (1970) noted that *Trichopeltarion nobile* begins differential growth of the major chela at 50–60 mm length. Specimens of three different species of *Trichopeltarion* that reach larger sizes have a major chela in most adult males observed (Table 4). Many of the smaller species have a large major chela; for example, *T. corallinus*, whose carapace is 24.5 mm long, and *T. glaucus*, whose carapace is 16 mm long. The major chela exhibits a similar morphology between certain species. *Trichopeltarion fantasticum*, *T. nobile*, *T. greggi*, *T. alcocki*, and *T. wardi* all have a chela that is morphologically similar, having straight edges, a triangular propodus, and being somewhat flattened. Several others, *T. balssi*, *T. glaucus*, and *T. sagamiensis*, have a major chela that has rounded edges, and is more swollen and bulbous rather than flattened.

While many of the species previously recognized as *Trachycarcinus* are more circular than most species under consideration, there is a possible size constraint that may explain the pentagonal outline of several species. The species discussed here span a wide range of adult sizes (Table 5). *Trichopeltarion nobile* has been reported to grow up to 83 mm long (Pequegnat, 1970), compared to the adult form of *Trichopeltarion glaucus* which measures 16 mm in length (Guinot, 1989, Pl. 5, fig. D). It is possible that size of the carapace may play a role in definition of the outline as pentagonal or subcircular. Smaller individuals tend to be more pentagonal. The overall size of the organism affects characters other than outline. Tubercle density and carapace ornamentation are commonly affected by carapace size

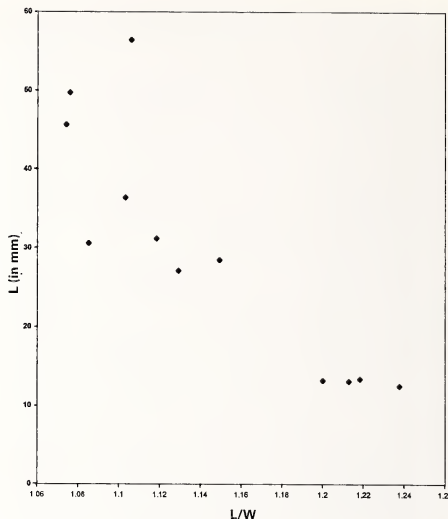


Figure 15. Measurements taken on a population of twelve *Trichopeltarion fantasticum* from BS774, 30 km ENE of Castlepoint, NZ. Specimens were collected at a depth of 278–283 m at NZOI station R132 and are the possession of the National Museum of New Zealand. No catalog numbers are assigned to the specimens. Length measurements are taken excluding frontal spines, and width measurements exclude lateral spines. The distribution of points approximates a logarithmic curve and indicates anisometric growth.

within this group. Many of the smaller species within the genus possess characters that are similar to the characters possessed by the juveniles of *T. fantasticum*. It is possible that juvenile characters of the genus are retained in several species due to paedomorphism. Progenesis, or paedomorphism, may have lead to direct speciation. The possession of juvenile characters within the genus adds to the range of variation, making the classification of this group complex.

Anisometric growth was observed and can be readily demonstrated within a population of *T. fantasticum* (Figure 15). The carapace lengths of 12 individuals, measured from the base of the frontal spines to the posterior margin, ranged from 10 mm to 56 mm. The smaller the specimen, the more pentagonal it appeared (Figure 16). The smaller, more pentagonal specimens bear a striking resemblance in outline to *Trichopeltarion corallinus*, which was small, measuring 24.5 mm in length excluding frontal spines. Larger specimens of *T. fantasticum*, measuring up to 69 mm in length, have circular outlines almost identical to *T. nobile*. The par-



Figure 16. Six specimens of *Trichopeltarion fantasticum* (A–F) showing a decrease in pentagonal outline with an increase in size. National Museum of New Zealand, Wellington, specimens from station R132, no catalog number. Scale bar equals 1 cm.

ticular male specimens also have an enlarged major cheliped as in many mature male specimens of *T. nobile*. The anisometric growth observed in *T. fantasticum* can explain the pentagonal outline of the smaller specimens and the circular outline of the larger specimens. The pentagonal outline is a function of the curvature of the anterolateral margin. The wider the specimen, the longer and more curved the anterolateral margin. The pentagonal species in question are believed to be adult forms, and thus would not be expected to develop a circular outline due to their small sizes. This is a probable example of paedomorphism. The smaller the carapace, the more pentagonal the outline of the carapace.

Not only was shape of the carapace affected by the size, or age, of the specimens of *Trichopeltarion fantasticum* studied, but also was the degree of tubercle density. There has been a considerable amount of emphasis placed on the degree of ornamentation of the carapace, especially around the margins, when diagnosing the two genera. When observing the wide range of specimens it is obvious that *T. nobile* is the least ornamented. It is generally described as smooth, excluding the margins and the tops of several swellings that mark regions. Many of the species previously referred to *Trachycarcinus* have a dense covering of tubercles, as do a few species of *Trichopeltarion*, namely *T. wardi* and smaller specimens of *T. fantasticum*. Smaller specimens of *T. fantasticum* have much more dense ornamentation, with the raised pustules that define regions appearing to be more pronounced. The density of tubercles of small specimens of *T. fantasticum* approaches that of the dense and defining ornamentation of *Trachycarcinus*. The larger the specimens of *T. fantasticum* become, the more sparsely ornamented they become. The tubercles and swellings covered with granules become more spread out, and the pustules do not display as much relief. The larger specimens of *T. fantasticum* approach the smoothness of *T. nobile*, and display an almost identical pattern of ornamentation (Figure 17). While this may not be the case with every species observed, it is the rule that the larger the specimens, the less dense the ornamentation. Because *T. nobile* is the largest of the extant species, it fits the expectation that the larger the carapace length, the smoother the carapace surface. The larger, less ornamented specimens of *T. nobile* would then have to be considered an exception with smaller sized, more densely ornamented carapaces as the norm for this group. While there are several types of ornamentation observed within the genus previously known as *Trachycarcinus*, the aforementioned observations only address density of ornamentation.

In the case of *Trichopeltarion* and *Trachycarcinus*, juvenile characters retained within *Trachycarcinus* (shape, degree of ornamentation, long spines on margins), previously have been considered to be morphological differences between the two genera, rather than morphological variations within one genus. It could be that paedomorphosis, specifically progenesis, led to speciation within this genus.

TRICHOPELTARION NOBILE A. Milne Edwards, 1880

Figures 17B, 18

Trichopeltarion nobile A. MILNE EDWARDS, 1880, p. 20, Pl. 2; RATHBUN, 1930b, p. 168, Pl. 73; PEQUEGNAT, 1970, p. 184–187, fig. 6–4, 6–5.

Trachycarcinus spinulifer RATHBUN, 1898, p. 278, Pl. 6, fig. 1 (cat. no. 9639 USNM); 1930b, p. 166, pls. 70, 71, figs. 26, 27.

Diagnosis

Carapace slightly longer than wide excluding lateral spines; surface thickly velvety as in *Dromia*, especially in female. Median frontal spine shorter than lateral ones, essentially an equilateral triangle. (After Rathbun, 1930b, p. 168).

Measurements

Male holotype: length of carapace 66 mm, width of same including spines 77 mm, width without spines 65 mm; length of right cheliped 96 mm, of left cheliped 55 mm (Rathbun, 1930b).

Habitat

302–820 m (57° F at 302 m) (Rathbun, 1930b).

Distribution

The holotype was taken off St. Lucia of the Caribbean Sea, station 219, U.S.C.S.S. *Blake* (MCZ 3054) (Rathbun, 1930b). Gulf of Mexico off the coast of the Mississippi delta and all other parts of the Gulf except the SE quadrant (Pequegnat, 1970).

Remarks

Study of specimens of *Trichopeltarion nobile* and *Trachycarcinus spinulifer* from the U. S. National Museum of Natural History reinforces the conclusion of Pequegnat (1970) that *Trachycarcinus spinulifer* should be synonymized with *Trichopeltarion nobile*. Rathbun's holotype for *T. spinulifer* was an immature male, while Edwards' holotype of *T. nobile* was a subadult male. The age, and thus size, differences between the two holotypes were the reason for placing them into two separate genera.

The morphological differences observed are due to age and size of the chelae. The major chela of mature males can reach an enormous size compared to the carapace size, about three times the size of the minor chelae. The immature male type of *Trachycarcinus spinulifer* had chelae of equal size. By comparison, a mature male of carapace length 68 mm had a major chela of 109 mm measured along the upper border. From measurements taken from Pequegnat (1970, p. 187), it can be concluded that the male does not start to grow the enlarged chela until the crab reaches 50–60 mm in length. The specimens observed in this study support this contention.

Although it was previously thought that only the right chela



Figure 17. A, *Trichopeltarion fantasticum*, dorsal view of a mature male from the National Museum of New Zealand, Wellington, no catalog number. B, *Trichopeltarion nobile*, dorsal view of mature male, USNM 128427. The two species exhibit similar outlines and ornamentation patterns. Scale bars equal 1 cm.

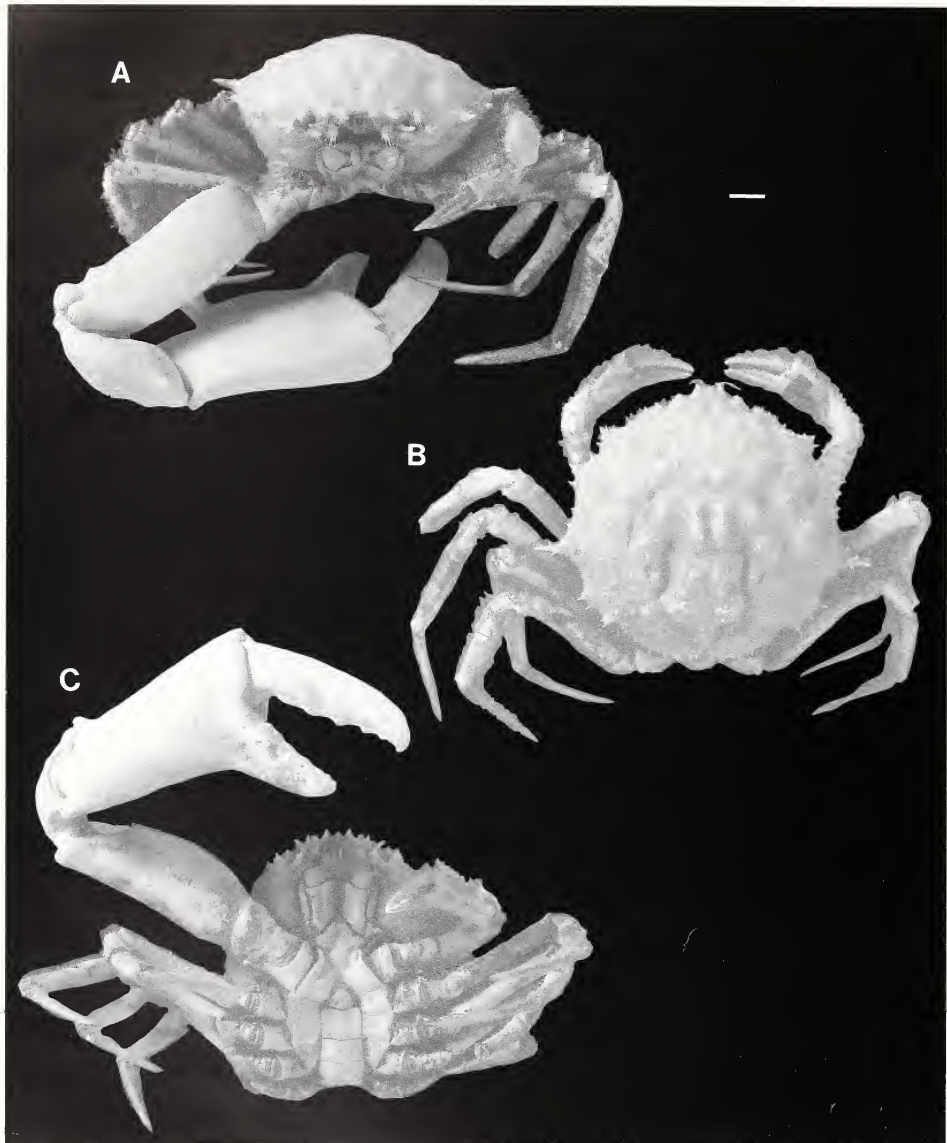


Figure 18. Orbital (A) and ventral (C) views of male *Trichopeltarion nobile*, USNM 128427. B, Dorsal view of female *Trichopeltarion nobile*, USNM 93674. Scale bar equals 1 cm.

grew to great size, it is now known that the left chela can be the large one in some males. In four of the 18 large males at Pequegnat's disposal the left chela was dramatically larger than the right. In four of the 12 large males of *Trichopeltarion greggi* studied herein the left chela is larger than the right chela.

According to the reexamination of the type specimen in the Museum of Comparative Zoology by Fenner A. Chace, the type has no median carina as described by A. Milne Edwards (Pequegnat, 1970). This observation was made by Pequegnat (personal communication with Henry B. Roberts, Smithsonian Institution).

Trichopeltarion nobile differs from all other species of *Trichopeltarion* by having a median frontal spine that is noticeably shorter than the lateral spines, and is an equilateral triangle. *Trichopeltarion nobile* differs from *T. wardi* and *T. fantasticum* by having the lip of the posterior margin adorned with a random series of singular spines, similar to the condition observed in well-preserved specimens of *T. greggi*. The lateral spines of *T. nobile* bear tiny spinelets and are cylindrical and long compared to the lateral spines of *T. wardi* and *T. greggi*. The lateral spines are triangular near the base, but do not have as many spinelets as *T. fantasticum*. In some specimens of *T. fantasticum*, the spines appear to be more cylindrical and longer.

The ornamentation of *T. nobile* consists of pustulose areas sometimes crested by granules. *Trichopeltarion nobile* seems to have two pustules in the anterior part of the cardiac region compared to only one in *T. fantasticum*, and none in *T. greggi*. Also, *T. nobile* and *T. greggi* have a double pustule located in the quadrilateral arrangement of the mesobranchial region as opposed to a singular pustule in *T. fantasticum*. The female specimen observed had many more granules on the raised areas than the two males. The raised areas are also much more distinct and granulose anteriorly compared to the males, whose anterior pustules lack granules.

Trichopeltarion nobile has two distinct compound spines located on the posterolateral margin, differing from *T. fantasticum* which has one large singular spine on the posterolateral margin. *T. greggi* seems to have two posterolateral spines located in the same general area, but this has been observed in only two of the best preserved specimens. They do appear to be compound and large in the larger specimens.

The female specimen studied has a thicker coat of velvet on the surface of the carapace compared to the two males. The males have an even coat, but the carapace is visible. The female hair is so thick that the carapace is not visible on the dorsal surface; only the raised granulated pustules appear above the velvety mat. This is similar to the surface of a female *Trichopeltarion ovale*. It was also noticed that the carapace surfaces of *T. fantasticum* were somewhat more dense with hair on females than males.

TRICHOPELTARION OVALE Anderson, 1896

Figure 19

Trichopeltarion ovale ANDERSON, 1896, p. 103; ALCOCK AND ANDERSON, 1896, Pl. 25, fig. 4, 4a; RICHARDSON AND DELL, 1964, p. 146, 150; SAKAI, 1965, p. 44, Pl. 6, fig. 7; SAKAI, 1976, p. 314, Pl. 103, fig. 2.; SERENE AND VADON, 1981, p. 122, 126.

Trichopeltarion ovale ALCOCK, 1899, p. 57; ALCOCK AND MACGILCHRIST, 1905, Pl. 75, fig. 1 a-c.

Trachycarcinus ovale SERENE AND VADON, 1981, p. 122, 126. GUINOT, 1989, p. 355-360, fig. 2, A-D fig. 3, A-D, Pl. II, A-E.

Type Locality

Southeast of Sri Lanka [Ceylon], 6°50'20" N, 79°36'20" E, *Investigator*, station 204, 180-217 fathoms (Guinot, 1989, p. 355).

Habitat

100-600 m (Guinot, 1989, p. 355).

Distribution

Southeast of Ceylon (300-400 m depth). Strait of Makassar, station 214, 0°31'4" N, 117°50'1" E (600 m). Japan (100-200 m). Philippines, station 43, 13°50'5" N, 120°28'0" E (500 m) (Guinot, 1989, p. 355, 358).

Remarks

Guinot (1989) believed that *Trichopeltarion ovale* actually belonged to *Trachycarcinus*, with the specimens from the Philippines representing a possible subspecies.

TRICHOPELTARION FANTASTICUM Richardson & Dell, 1964
Figures 16, 17A, 20

Trichopeltarion fantasticum RICHARDSON AND DELL, 1964, p. 145-151, figures 1-11.

Holotype

Adult male from VUZ 42 in Dominion Museum, Wellington (Cr. 1322).

Type Locality

Stations of Zoology Department, Victoria University of Wellington: VUZ 42, 41°32'30" S, 174°52' E, Palliser Bay in c. 100 fathoms, 19 January 1956. For additional localities see Richardson and Dell, 1964, p. 149-150.

Measurements

Measurements (in mm) of a single population within the species are plotted in Figure 15.

Distribution

In New Zealand, from Kaipara on the west coast and the Bay of Plenty on the east coast to as far south as Foveaux Strait and Fiordland, and off the coast of the Chatham



Figure 19. Ventral (A), orbital (B), and dorsal (C) views of *Trichopeltarion ovale*, USNM, from station 5423, no catalog number. Scale bar equals 1 cm.

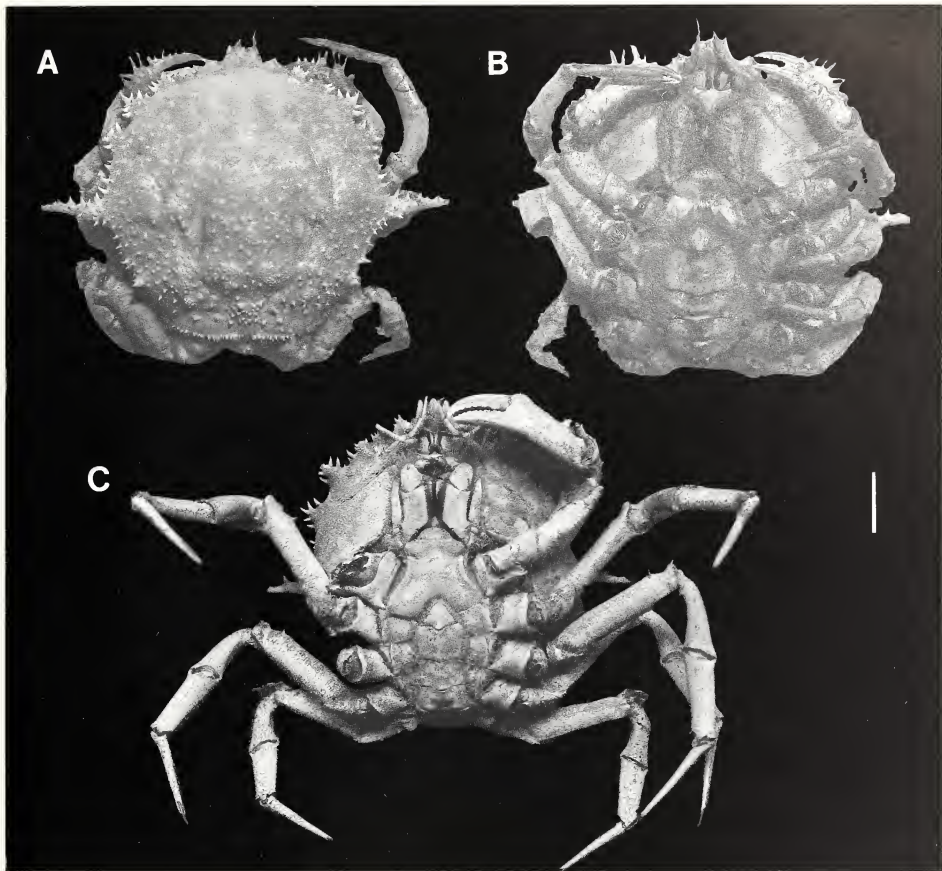


Figure 20. Dorsal (A) and ventral (B) view of mature female *Trichopeltarion fantasticum*, Cr. 6083; C, ventral view of mature male from National Museum of New Zealand, Wellington, no catalog number. Scale bar equals 1 cm.

Islands (Richardson and Dell, 1964, p. 149–151).

Habitat

Typically found at depths of 200–800 m. It is also found frequently on the continental shelf at shallower depths (Richardson and Dell, 1964, p. 150).

Remarks

Trichopeltarion fantasticum differs from the other species of *Trichopeltarion* by having a carapace length, including the

frontal spines, that is noticeably greater than the carapace width, excluding the lateral spines. Richardson and Dell (1964) measured seven specimens of *T. fantasticum* that had a mean length, including the frontal spine, of 46.8 mm, and a mean width, excluding lateral spines, of 39.1 mm. Measurement of eight adult specimens from the National Museum of New Zealand, yielded a mean length, excluding the frontal spines, of 38.2 mm, and a mean width, excluding the lateral spines, of 34.7 mm. While the length of the carapace appears to be somewhat greater than the width, the carapace broadens with age.

The juvenile specimens are considerably less wide than long, as seen in Figure 15. This also holds true for *T. nobile* (Pequegnat, 1970), and can lead to misinterpretations of carapace shape due to the age and size of the specimen.

While *Trichopeltarion fantasticum* appears to be similar to *T. greggi* with regard to the nature of the anterolateral and lateral compound spines, it differs by having the central frontal spine of equal or slightly greater length than the lateral frontal spines. *Trichopeltarion greggi* has a shorter central spine. Although Richardson and Dell (1964) diagnosed *T. fantasticum* with a central frontal spine longer than the two lateral spines, this was observed in only two of the twenty specimens examined. The majority had a central frontal spine that was approximately the same length as the lateral frontal spines. The ornamentation of *T. fantasticum* is also much more complex than in *T. greggi*.

Trichopeltarion fantasticum differs from *T. wardi* by having a larger mean length/width ratio, and longer, sharper lateral spines. The lateral spines of *T. fantasticum* appear to be the longest of the species, proportional to the carapace size, and are also the most cylindrical in shape. *Trichopeltarion nobile* exhibits a more circular carapace that is not as heavily ornamented, and a much larger mean size of the carapace.

Trichopeltarion fantasticum has a distinct granule-bearing tubercle pattern on the dorsal surface of the carapace (Figures 16, 17, and 20). This pattern can be seen in other species of *Trichopeltarion*, but differs slightly in tubercle size and granule density. The pustules, or raised areas, are more pronounced in juveniles and smaller specimens. This was observed primarily within *T. fantasticum*, but is believed to be the case for all species of *Trichopeltarion*. As the size of the carapace increases, the raised areas are not as pronounced or topographically high. They ascend more gently from the carapace surface and may blend into other raised areas forming an agglomeration of raised areas.

Trichopeltarion fantasticum has a large posterolateral spine, distinguishable from the smaller spine on the margin. It appears to be cylindrical, widening at the base. The spine is singular, although it may have spinelets at the base. *Trichopeltarion nobile* has distinct posterolateral spines located in the same position along the margin. The difference is that *T. nobile* has two posterolateral spines, both of which widen at the base and are compound. *Trichopeltarion greggi* has at least one distinct large posterolateral spine that appears singular, with possible spinelets at the base. This feature is not commonly preserved on *T. greggi*, but one very large male has two distinct large triangular posterolateral spines. The preservation does not permit identification of the spines as being singular or compound, because the tips are broken off.

The posterior margin of *T. fantasticum* is formed of a thin lip with a row, or line, of dense granules. All species of *Trichopeltarion* seem to have some type of lip on the posterior margin, but the type and density of ornamentation varies. *Trichopeltarion wardi* has a very dense accumula-

tion of tubercles, while *T. nobile* and *T. greggi* seem to have randomly placed, sparsely dispersed, semi-triangular spines, rather than granules or tubercles. *Trichopeltarion ovale* has a dense row of very sharp and cylindrical spines.

Male specimens of *Trichopeltarion fantasticum* appear to be less hairy on the dorsal carapace surface than the females. This feature was also noticed in the specimens of *Trichopeltarion nobile* (= *Trachycarcinus spinulifer*), on which the males had a fine velvet on the carapace surface, and the females had a dense mat of hair through which the carapace cannot be seen. Only the raised granulated areas standing above the hair are visible, as in the female specimen of *T. ovale*. The adults of *T. fantasticum* are considerably more hairy than the juveniles. This may be true in other species of the group, but no juveniles were observed except those of *T. fantasticum*.

TRICHOPELTARION WARDI Dell, 1968

Figure 21

Holotype

Holotype male in Australian Museum, Sydney (P. 14789), and one paratype male in the Dominion Museum, Wellington (ex Melbourne Ward collection).

Type localities

Off of Maria Island, Tasmania; off Cape Everard, Victoria, 38°12.5' S, 149°05.5' E (Dell, 1968, p. 276).

Depth

80 to 140 m (Dell, 1968).

Distribution

Off Maria Island, Tasmania, to Victoria, Australia (Dell, 1968).

Remarks

The species seems closest to the New Zealand species, *Trichopeltarion greggi*, by having the anterolateral spines of similar size, arrangement, and compound nature. It differs from *T. greggi* by having fewer spinelets on the lateral spine, and a more dense ornamentation of larger tubercles. The degree of ornamentation density present on *T. wardi* is much greater than on *T. nobile*, *T. fantasticum*, or *T. greggi*. The axial carapace regions are distinct and recognizable, as they are in the other species of *Trichopeltarion*.

The tridentate front of *T. wardi* differs from the fronts of all other species of *Trichopeltarion* by being very large and pronounced compared to the anterolateral spines. The lateral spine of *T. wardi* differs from all of the other species of *Trichopeltarion* by being very short relative to carapace width. *Trichopeltarion wardi* has no spines posterior to the lateral spine, only a few tubercles. Unlike *T. nobile*, the right chela is the only one that was observed to be greatly devel-

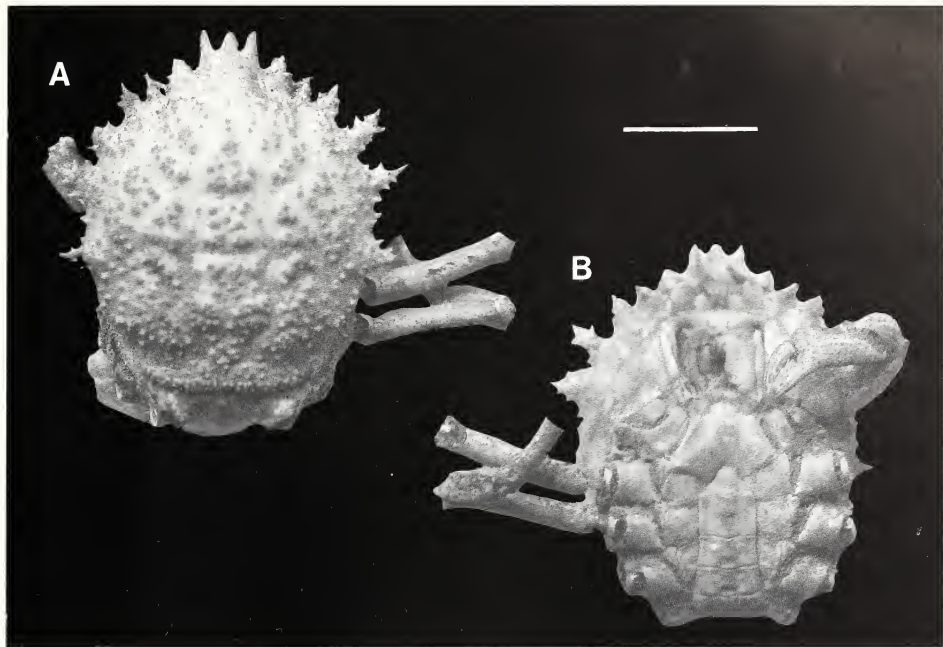


Figure 21. *Trichopeltarion wardi*, Cr. 1854. Dorsal (A) and ventral (B) views. Scale bar equals 1 cm.

oped in the males. *Trichopeltarion wardi* lacks the long lateral spines of *T. fantasticum*, *T. nobile*, and *T. greggi*. While Dell (1968) suggested that *T. wardi* had a simpler supraorbital spine than *T. fantasticum*, the supraorbital spine appears to be very similar morphologically. This becomes, in fact, a unifying character in *Trichopeltarion*.

TRICHOPELTARION BALSSI (Rathbun, 1932)

Figure 22

Trachycarcinus balssi, RATHBUN, 1932 p. 36; SAKAI, 1935, p. 141, Pl. 41, fig. 3; SAKAI, 1939 p. 432, Pl. 52, fig. 3; SAKAI, 1965, p. 108, Pl. 49, fig. 3; SAKAI 1976, p. 311–312, Pl. 102, fig. 2; RICHARDSON AND DELL, 1964, p. 146; TAKEDA, 1973, p. 12. For additional synonymies see GUINOT, 1989, p. 350.

Holotype

Male specimen, USNM 65063, measuring 22.4 mm in width (Rathbun, 1932).

Type locality

Cape Rollin, Simushir Island (46°46'40" N, 151°41' E). Albatross station 4801.

Depth

220 m (Rathbun, 1932, p. 36).

Habitat

Coarse black sand, pebbles (Sakai, 1976, p. 311–312).

Distribution

Japan, Isles of Tsushima, de Coree (Sakai, 1976, p. 311–312).

Remarks

The specimen observed, USNM 65058, has a very dense mat of mud-covered hair between the raised granules. The ornamentation style is different from all other *Trichopeltarion* species. The granules/tubercles are very large and rounded posteriorly, becoming smaller anteriorly. In the anterior regions of the carapace they are not rounded

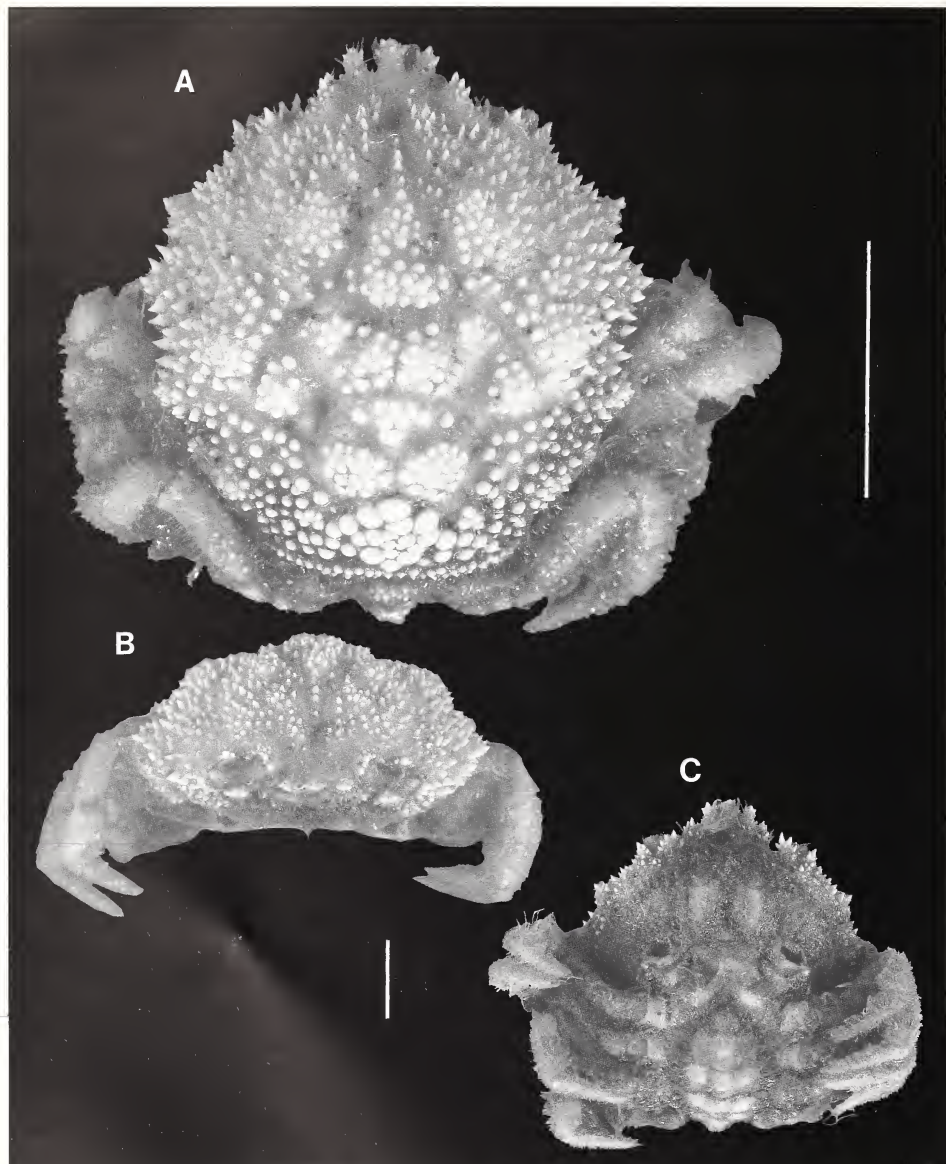


Figure 22. *Trichopelturion balssi*, USNM 65058. Dorsal (A), orbital (B), and ventral (C) views. Scale bars equal 1 cm.

tubercles, but are spinelike. No other species of *Trichopeltarion* has such a wide range of variation of tubercle shape upon a single carapace.

TRICHOPELTARION GREGGI Dell, 1969

Figure 23, 24, 25, 27

Diagnosis

Trichopeltarion with trifold front of equal length spines, constructed of grouped barbs; four distinct agglomerate tubercles on urogastric region, carapace ornamented by singular tubercles becoming more dense posteriorly.

Description

Carapace subcircular, approximately as wide as long; arched transversely and strongly arched longitudinally. Front of three prominent teeth almost of equal length. Central tooth slightly wider toward the base than those on either side. All spines, excluding those of front, arranged in groupings with spine group termed a spine, and each apex termed a barb of that spine. Inner orbital spine separated from tridentate front by very shallow notch, triangular in outline, five to six barbs. First barb directed obliquely adaxially, second directed forward, remaining barbs directed abaxially as they slope down the outer margin of the spine. Most forward projection of barbs measures one half length of frontal teeth. Orbits large, directed forward (Figure 24A). Orbital spine separated from inner orbital by deep notch. Spine rectangular in outline, not widening significantly toward base. Four to five barbs crest the summit of the spine, directed forward, smallest of all marginal spines, length extends anteriorly to base of tridentate front. Outer orbital spine triangular in outline, separate from orbital spine by shallow notch. One to two barbs on each slope of spine, both spine and barbs directed forward.

Anterolateral margin rounded, with two large triangular spines. First spine separated from outer orbital spine by a shallow notch, five to six barbs becoming smaller toward base. Second spine not as well developed, arcuate outline does not protrude from margin as prominently, five to seven barbs present. Two small singular spines anterior to large triangular lateral spine. Lateral spine steeply triangular, one central barb, three to four barbs arise from each slope of the spine. Posterolateral margin straight to gently curved, extends obliquely into posterior margin, ornamented with three to six small singular spines which become smaller posteriorly. Posterior margin curves concave axially, vaulted when viewed from posterior, ornamented with small singular evenly-spaced spines.

Carapace uniformly and finely punctate, with numerous short, conical tubercles concentrated in posterior half. Well-defined branchiocardiac grooves. Frontal region generally smooth. Protogastric region slightly tuberculate to smooth. Mesogastric with axial pattern of four tubercles, anterior-most tubercle followed by another simple tubercle,

two additional tubercles in widest part of region lie on opposite sides of the midline. Urogastric with four distinct conical tubercles forming trapezoidal outline, two anterior-most tubercles being more widely spaced than posterior two. Tubercles singular, or grouped, never crested by granules. Cardiac region lyrate, densely tuberculate to nearly smooth, widest posteriorly, culminating in two bulbous swellings. Branchiocardiac groove terminates in pit anteriorly. Intestinal region small, rounded, sometimes tuberculate. Hepatic region marked by conical swelling sometimes bearing tubercles. Branchial regions not distinct. Epibranchial region smooth to sparsely tuberculate. Mesobranchial sparsely to densely tuberculate. Metabranchial always most densely tuberculate.

Pterygostomial concave from posterior corner of buccal cavity to intersection with carapace below second posterolateral spine; finely granulate, most dense anteriorly.

Sternum ovoid; longer than wide, maximum width attained at separation of somites five and six (Figure 24C). Somites one–three distinct, forming triangular plate. Somite four largest, diamond shaped. Somites five–seven similar in outline, directed obliquely posteriorly, decreasing in width posteriorly. Somite eight narrower, poorly preserved.

Buccal frame nearly rectangular, somewhat wider anteriorly. Third maxillipeds poorly preserved.

Abdomen of male with equilateral triangular telson, weakly swollen distally; somites five and six fused, widening proximally, raised axial regions; somites four and three similar in shape, decrease in width proximally, raised axial regions; abdominal somites two and one comparable in width, poorly preserved (Figure 25).

Chelipeds massive. Hand triangular, length of hand about two times height and five times thickness, upper and lower margins sharp. Fixed finger curved, stout at base, about 55 percent total length of propodus. Dactylus longer, more slender at base, more sharply curved than fixed finger. Denticles not apparent.

Coxae ovoid in cross section; coxa one large, coxae two–four equal in size and approximately one-half as large as coxa one, coxa five smallest.

Measurements

Measurements are given in Table 6. Position and orientation of measurements are shown on Figure 26.

Holotype

Trichopeltarion greggi Dell, 1968. Canterbury Museum, zfc 36. Adult measuring 71 mm in width (including lateral spines). The locality is situated one mile west of the mouth of the Motunau River, North Canterbury, New Zealand. The fossils are presumed to be from the Greta Siltstone which is middle–late Miocene (Feldmann and Keyes, 1992).

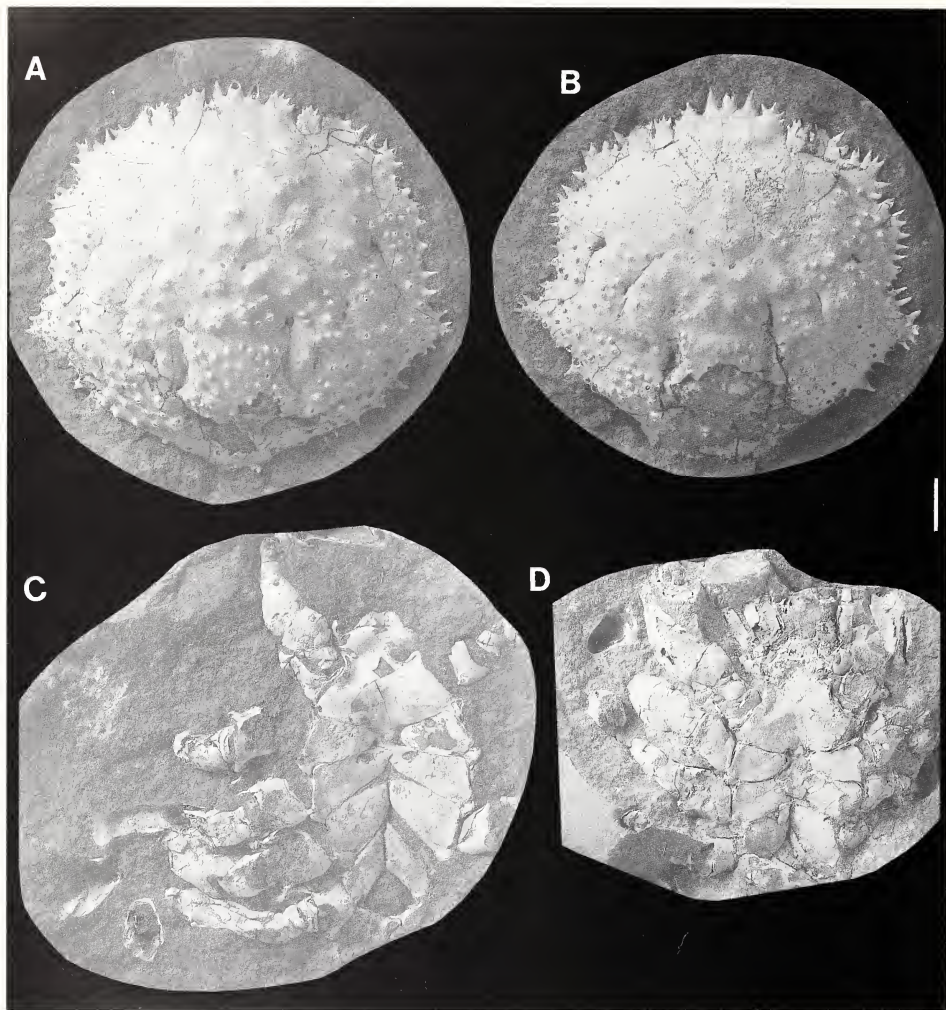


Figure 23. *Trichopeltarion greggi*. A, Dorsal view of DM 12; B, dorsal view of DM 48; C, ventral view of zfc 56; D, ventral view of AD 130. Scale bar equals 1 cm.

Localities and stratigraphic position

Specimens have been collected 1.6 km west of the mouth of the Motunau River, North Canterbury, New Zealand. Grid reference N34/147958. The majority of specimens are

from concretions lying on the beach, having been derived from the Greta Siltstone horizon in cliffs (Feldmann and Keyes, 1992). Based upon the following evidence, Feldmann and Keyes (1992) adopted the age of middle-late

Table 6. Maximum, minimum, and mean measurements (in mm) taken on 140 specimens of *Trichopeltarion greggi* obtained from the Canterbury Museum, the Institute of Geological and Nuclear Sciences Limited, and various private collections. Positions and orientations of measurements are illustrated in Figure 26.

	L1	L2	L3	L4	L5	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12
Minimum	39.09	35.72	17.18	19.85	38.00	5.23	13.84	17.84	26.78	35.94	8.92	11.12	36.65	40.99	41.00	19.26	2.23
Mean	66.74	62.80	27.44	33.64	69.21	7.35	21.25	29.64	42.91	57.17	15.65	19.47	61.18	70.09	66.64	27.71	3.71
Maximum	91.24	85.20	33.04	48.92	96.00	8.73	28.95	40.30	57.37	76.84	25.06	28.23	84.58	91.18	92.00	45.08	4.73

Miocene (Waiau-Tongaporutuan) for the Greta Siltstone with fossiliferous concretions. Lewis (1976) outlined the complex geology of the area which has debris flows containing clasts of "Greta Siltstone" which are late Pliocene (Waipipian), middle-late Miocene (Waiau-Tongaporutuan), and Early Miocene (Otaian-Altonian) age (see

also Fordyce, 1982, p. 651, 653). There is a greater age range of beds comprising "Greta Siltstone" represented than originally considered. Feldmann and Keyes (1992) believed that the presence of concretions containing *Tumidocarcinus giganteus* Glaessner would support an age of early-late Miocene with a middle-late Miocene age being favored.

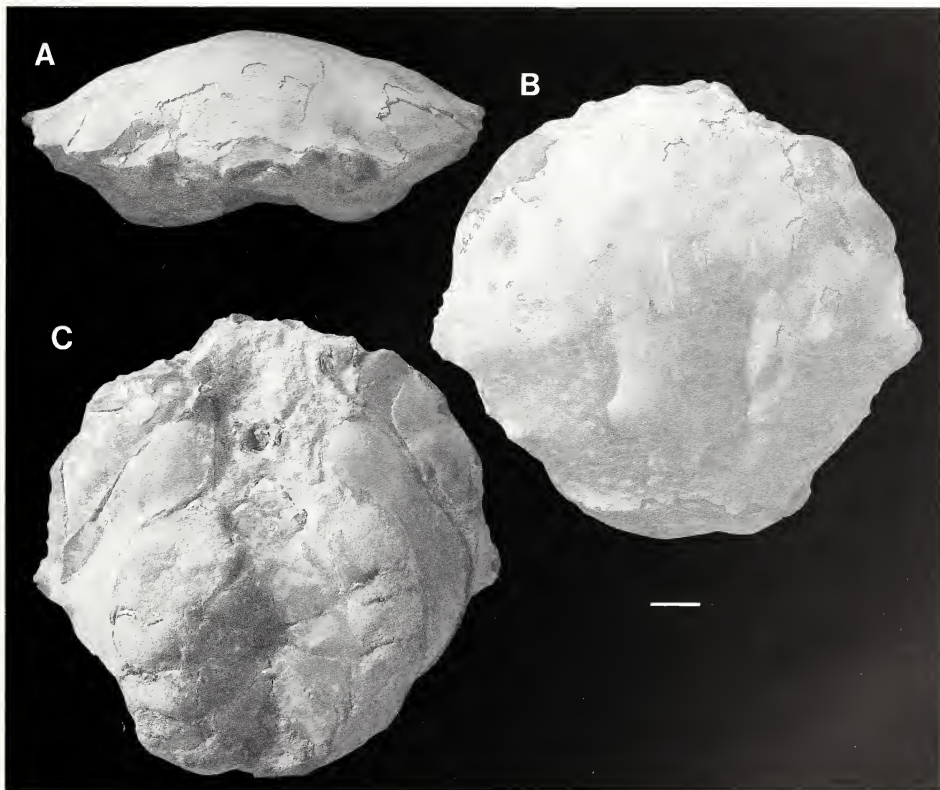


Figure 24. *Trichopeltarion greggi*, zfc 235. Orbital (A), dorsal (B), and ventral (C) views. Scale bar equals 1 cm.



Figure 25. Overall ventral view (A), and close-up of abdomen (B), of mature male *Trichopeltarion greggi*, DM 65. Scale bars equal 1 cm.

Remarks

Trichopeltarion greggi is a species known only from the fossil record. It appears to be very closely related to *T. nobile*. The anterolateral spines, lateral spines, two distinct posterolateral spines, and sparsely spined posterior margin are very similar in nature. *Trichopeltarion greggi* also has a very smooth carapace surface with granulation becoming more dense posteriorly, starting in the hepatic region. *Trichopeltarion nobile* is covered with a fine velvety hair. Although hair is not preservable in the fossil record, some evidence of it may survive: the carapace surfaces in several specimens of *T. greggi* (Figure 27) have evidence of hair. If this is a correct interpretation, then *T. greggi* would have had a dense coat of possibly velvety hair as is found in *T. nobile*. The most notable differences between *T. greggi* and *T. nobile* are the short axial frontal spine of *T. nobile* and the lack of two pustules in the anterior part of the cardiac region in *T. greggi*.

The tubercle pattern found on *T. fantasticum*, *T. nobile*, and to some extent in *T. wardi*, also exists in *T. greggi*. The main difference is that *T. fantasticum* has one pustule in the anterior part of the cardiac region, *T. nobile* has two pustules in that area, and *T. greggi* does not have any observable raised pustules in the anterior part of the cardiac region, only granules. The major chela of *T. greggi* is very similar to that of *T. nobile* in size and shape.

There are some major differences between the living species endemic to New Zealand, *T. fantasticum*, and the fossil species endemic to New Zealand, *T. greggi*. The relative shape and proportional size of the lateral spine is different. The degree of granulation anteriorly is more dense in *T. fantasticum*, while *T. greggi* has a smooth carapace surface towards the front. The posterolateral spines and spinosity of the posterior margin are also different.

Genus *ATELECYCLUS* Leach, 1814

Type species

Atelecyclus rotundatus (Olivi, 1792) = *Cancer* (*Hippa*) *septemdentatus* Montagu, 1813.

Diagnosis

Carapace subcircular to weakly pentagonal with anterior half subcircular, several teeth with tiny spinelets on lateral margins. Front with three teeth. Basal antennal article united to inner margin of suborbital region and to front, thus separating orbit entirely from antennular pit, latter being excavated in front. Antennal flagella well developed. Third maxillipeds cover whole mouth-field and extend forward to the base of the antennae. (Modified from Christiansen, 1969.)

ATELECYCLUS ROTUNDATUS (Olivi, 1792)

Cancer rotundatus OLIVI, 1792, p. 47–48, Pl. 2, fig. 2.

Cancer (*Hippa*) *septemdentatus* MONTAGU, 1813, p. 1–2, Pl. I, fig. 1.

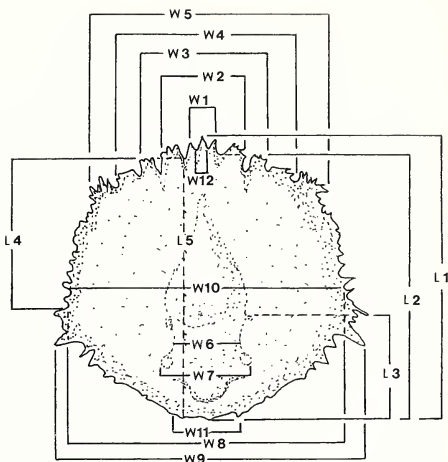


Figure 26. Position and orientation of measurements taken on 140 specimens of *Trichopeltarion greggi*.

Atelecyclus heterodon LEACH, 1815, Pl. II, fig. 1–5.

Atelecyclus septemdentatus A. MILNE EDWARDS AND BOUVIER, 1900, p. 60–61, and of many other authors.

For a more complete list of synonyms, see Monod (1956).

Type locality

Golfo di Venezia, northern Adriatic (Christiansen, 1969, p. 37–39).

Habitat

Recorded on sandy and soft bottom between 15–40 and 190–324 m (Christiansen, 1969, p. 37–39).

Distribution

West and South coasts of Norway, with the northernmost record at Grip; northern part of Swedish western coast; Belgium; E. coast of British Isles; Faeroe Banks; Shetland; northern part of North Sea; E. coast of Atlantic from the Cape Verde Islands to the Hebrides; Mediterranean; S. Africa (Christiansen, 1969, p. 37–39).

Remarks

Confusion has existed with regard to identification of the two East Atlantic species of *Atelecyclus*, *A. rotundatus* and *A. undecimdentatus* (Herbst), and was resolved by Forest (1958) (Christiansen, 1969). Forest (1958) noted that *A. undecimdentatus* is always wider than long, while *A. rotundatus* is always longer than wide.

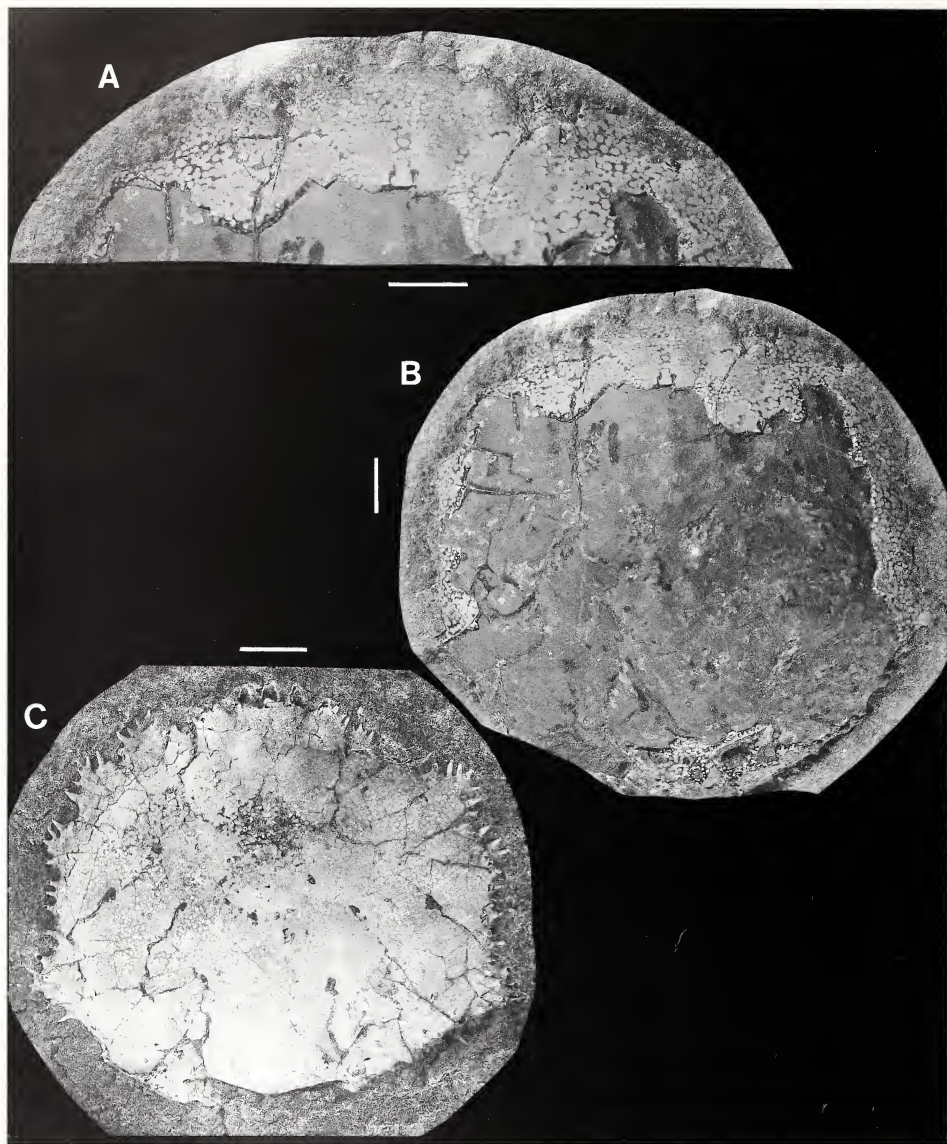


Figure 27. *Trichopeltarion greggi*. A, B, Mottled pattern of circular markings on the remaining cuticle of zfc 108. The majority of zfc 108 is preserved as an internal mold. C, DM specimen possessing cuticle that shows onset of the mottled pattern. Scale bars equal 1 cm.

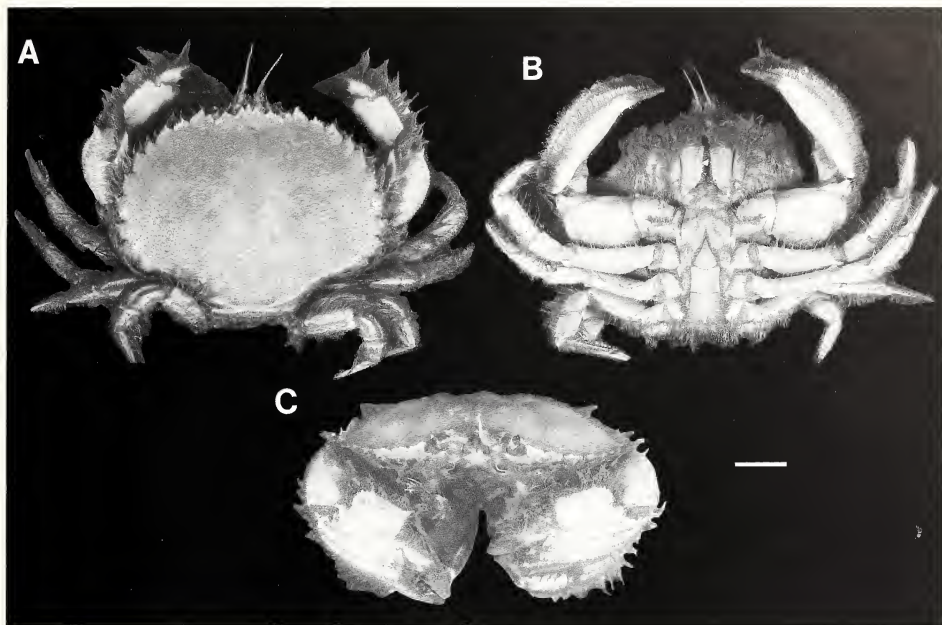


Figure 28. *Atelecyclus undecimdentatus*, USNM 121861. Dorsal (A), ventral (B), and orbital (C) views. Scale bar equals 1 cm.

ATELECYCLUS UNDECIMDENTATUS (Herbst, 1783)

Figure 28

Cancer undecimdentatus HERBST, 1783, p. 181.

Distribution

This species is found only in the East Atlantic Ocean. Localities include the Gulf of Gascogne, coast of Gabon, and Gambia. Forest (1958) believed the species to be rare or absent in the Mediterranean Sea.

Remarks

This species differs from *Atelecyclus rotundatus* primarily by possessing a carapace shape that is wider than long. The length-to-width ratios of *A. rotundatus* range from 0.93 to 1.03, while the ratios of *A. undecimdentatus* are from 0.76 to 0.86, respectively (Forest, 1958). This species is the only atelecyclid that is measurably wider than long. The shape of the carapace bears a superficial resemblance to that of *Cancer* Linnaeus.

Other species

The following species were not directly observed and cannot be verified as belonging to the genus *Atelecyclus*:

Atelecyclus rugosus Desmarest, 1822

Atelecyclus carniolicus (Bittner), 1883

Atelecyclus illyricus (Bittner), 1883 (Previously referred to *Cancer*.)

Atelecyclus elegans Ristori, 1896

Atelecyclus fraasi (Lőrenthey), 1909 (Previously referred to *Cancer*.)

Atelecyclus szontaghi Lőrenthey, 1929 in Lőrenthey and Beurlen, 1929 (This species has since been placed in the genus *Tasadia carniolica* (Bittner, 1884) by Janssen and Müller, 1985.)

Atelecyclus gorodiskii Gorodiskii and Remy, 1959

Only the literature available was used to verify generic placement, but many of the figures did not allow for clear observation of the necessary characters. Several of the species have been previously recognized as *Cancer*. A comprehensive study of the aforementioned species would be necessary to decipher the correct generic placement with regard to *Cancer* or *Atelecyclus*.

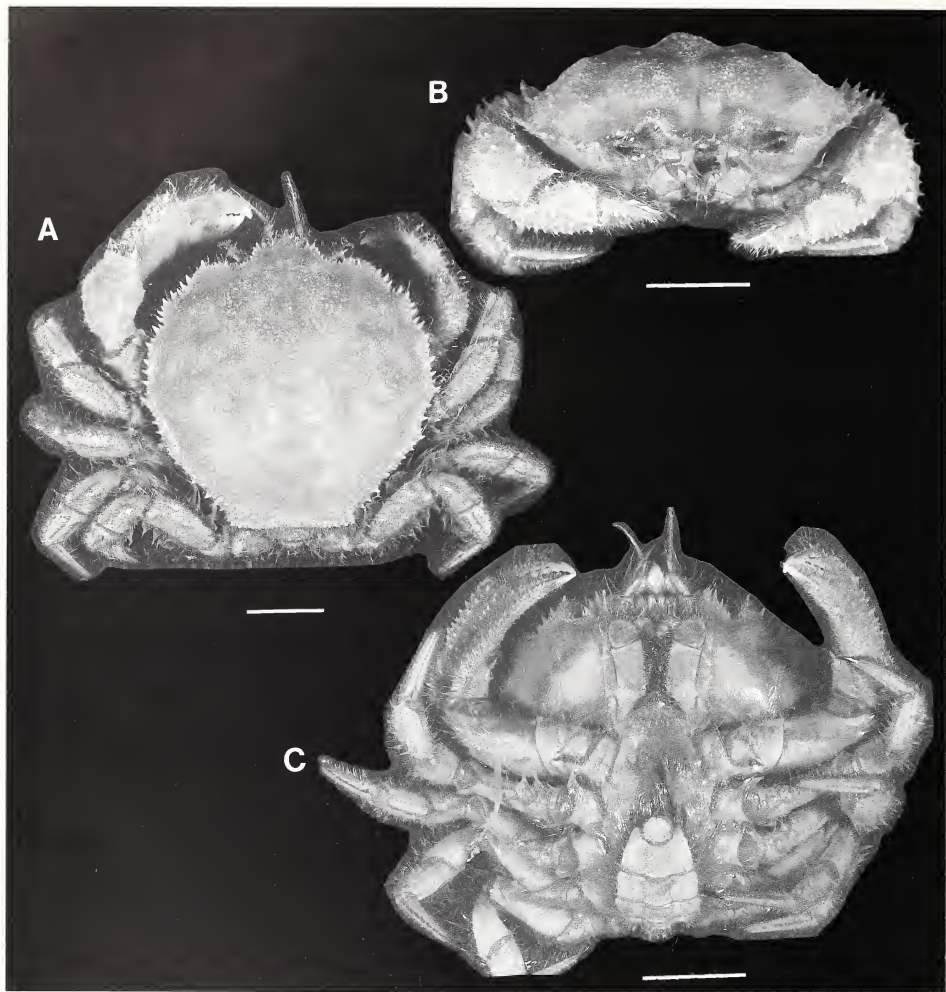


Figure 29. *Peltarion spinulosum*, USNM 152710. Dorsal (A), orbital (B), and ventral (C) views. Scale bars equal 1 cm.

Genus *PELTARION* Jacquinot, 1847

Atelecyclus WHITE, 1843, p. 345; NICOLET, 1849, p. 175.

Peltarion JACQUINOT, 1847, Pl. 8, figs. 1–3; WHITE, 1847, p. 52; DANA, 1852b, Pt. 1, p. 298; Pt. 2, p. 1425; STEBBING, 1900, p. 519; RATHBUN, 1930b, p. 160.

Hypopeltarium MIERS, 1886, p. 210; RATHBUN, 1897, p. 165.

Hypopeltarium ORTMANN, 1893, p. 421.

For additional information see Rathbun (1930b, p. 161–164).

Type species

Peltarion magellanicus Jacquinot, 1847 (= *Atelecycylus spinulosus* White, 1843).

Diagnosis

Carapace suborbicular or broad oval: anterior half broader; very convex, strongly deflexed anteriorly; surface rough, ornamented with tubercles, median sutures deep. Rostrum horizontal, triangular, tridentate, median tooth sometimes larger and more advanced than lateral. Anterior and lateral margins toothed, teeth compound with triangular outline. Orbits four-toothed. Eye stalks slender, curved, capable of concealment within orbits. Basal article of antenna very short, second article longer. Merus of third maxilliped somewhat longer than wide, broadly truncate at insertion of palp. Chelipeds stout. Carpus and propodus of legs of subequal length. Abdomen of male small, narrow. (Modified from Rathbun, 1930b, p. 161.)

PELTARION SPINULOSUM (White, 1843)

Figure 29

Atelecycylus spinulosus WHITE, 1843, p. 345.

Atelecycylus chilensis NICOLET, 1849, p. 175.

Peltarion magellanicus JACQUINOT, 1847, Pl. 8, figs. 1–3, 1853, p. 83.

Peltarion spinulosum WHITE, 1847, p. 52; DANA, 1852a, Pt. 1, p. 304; CUNNINGHAM, 1871, p. 494; A. MILNE EDWARDS AND BOUVIER, 1923, p. 306.

Hypopeltarium spinulosum MIERS, 1886, p. 211.

Hypopeltarium spinulosum ORTMANN, 1893, p. 421; LENZ, 1902, p. 758.

Occurrence

Peltarion spinulosum is found in shallow water to 155 m (Rathbun, 1930b, p. 161).

Distribution

South America, from Uruguay to the Straits of Magellan and to the Island of Chiloe, Chile, including the Bay of Valparaiso (Nicolet, 1849, p. 175); Falkland Islands; east coast of Mexico (Rathbun, 1930b, p. 161).

PELTARION DEXTRUM (Rathbun, 1898)

Figure 30

Hypopeltarium dextrum RATHBUN, 1898, p. 277, Pl. 6, fig. 2.

Peltarion dextrum RATHBUN, 1930b, p. 161–164, fig. 25.

Occurrence

Peltarion dextrum is found at depths of about 462 m (Rathbun, 1930b, p. 161).

Distribution

East coast of Mexico, off of Cozumel Island, Yucatan (Rathbun, 1930b, p. 161).

Remarks

Peltarion dextrum appears to be similar to *Trichopeltarion*, especially with regard to the orbital and anterolateral spines. The one significant difference is the lack of lateral spines in *P. dextrum*.

Genus *PTEROPELTARION* Dell, 1972

Type species

Pteropeltarion novaezelandiae Dell, 1972.

Diagnosis

Carapace pentagonal with simple, long lateral spine on each side and moderately elongate rostrum. Rostrum flattened, about one-fifth of carapace length, terminating in three broad spines with lateral spines longer than central spine, and bearing a group of long, slender, stiff hairs terminally. Carapace surface finely granular, especially toward margins. Orbit marked by weak, blunt supra-orbital spine and a more strongly developed post-orbital spine. Chelipeds in adult females and sub-mature males sub-equal in size although even in females right cheliped is hypertrophied. Legs long and slender, set with a row of feathery branched hairs along upper surface, dactylus with two rows of stiff, short hairs. Male and female abdomens of six segments plus telson. (Modified from Dell, 1972 p. 55–56.)

PTEROPELTARION NOVAEZELANDIAE Dell, 1972

Figure 31

Measurements

Length including rostrum, 16.75 mm. Width including lateral spines, 24.5 mm; excluding lateral spines, 11.25 mm. Length of right cheliped, 24.25 mm. Length of merus of right cheliped, 13.25 mm. Length of dactylus of right cheliped, 7.00 mm. Length of fourth ambulatory leg, 20.00 mm (Dell, 1972).

Occurrence

In deep water, muddy substrates, 499–903 m. The shape of this crab, elongate rostrum, and forwardly-placed mouth-frame suggests that this crab may burrow into soft substrates (Dell, 1972, p. 59).

Distribution

In deep water from the latitude of Auckland (37° S) to south of Stewart Island (50° S), both east and west coasts of New Zealand from 169°–176° E (Dell, 1972, p. 56, 59).

Remarks

This species has the defining characters of an atelecyclid.



Figure 30. *Peltarion dextrum*, USNM 9558. Dorsal (A) and ventral (B) views. Scale bar equals 1 cm.

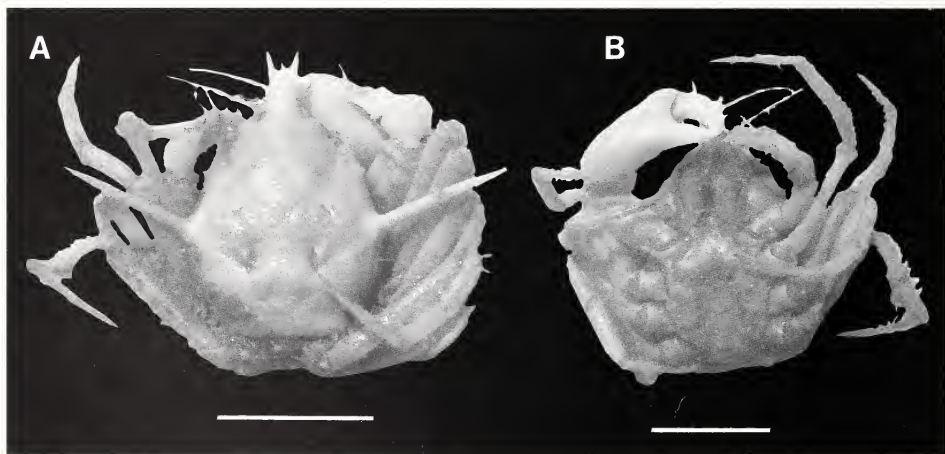


Figure 31. *Pteropeltarion novaezealandiae*, Cr. 7143. Dorsal (A) and ventral (B) views. Scale bars equal 1 cm.

It does, however, have other characters that suggest that it is a more derived form. Those characters are an elongate rostrum and the lack of prominent teeth on the anterolateral margins.

Genus *KRUNOPELTARION* Števcíć, 1993

Diagnosis

Carapace subcircular, convex. Lateral teeth triangular, apices elongated and narrowed, not sharply pointed. Dorsal surface of carapace covered with numerous smooth, apically rounded tubercles. One unpaired and several paired furrows on dorsal surface of carapace. Sternal

sutures four/five, five/six, and six/seven interrupted, seven/eight complete. (From Števčić, 1993, p. 1097.)

Type species

Krunopeltarion timorensis Števčić, 1993.

Measurements

Length 49.0 mm, 48.0 mm without rostral spines. Width 54.2 mm, 44.8 mm without lateral spines (Števčić, 1993, p. 1098).

Occurrence

The sole specimen, a female, of *Krunopeltarion timorensis* was collected at a depth of 270–300 m (Števčić, 1993, p. 1098). Deposited in the Northern Territory Museum of Arts and Sciences, Darwin, Australia.

Distribution

The one specimen of *Krunopeltarion* was collected in the Timor Sea by the F.V. "Endeavor Pearl" at Station Shot 3, 9°46' S, 130°14' E, on 15 September, 1987. Reg. No. NTM Cr. 006002. Coll. N.T. Fisheries Department (Števčić, 1993, p. 1098).

Remarks

Based on the figures and description of Števčić (1993), the classification of *Krunopeltarion* as an atelecyclid seems appropriate. Antennules fold longitudinally into a cavity, and are smaller than the antennae. The moveable part of the antenna is well developed, but does not fold upon itself. The orbits are made of a series of spines. Lateral margins bear teeth that are mostly compound. The carapace is not very broad, but is subcircular. The buccal region is elongate.

Sternal sutures four/five, five/six, and six/seven are incomplete, and suture seven/eight is complete. This is a character state that has not been observed within the atelecyclids in the past. However, all of the other characters conform to the previous diagnosis for the atelecyclids, so this feature serves to expand the diagnosis for the atelecyclids.

Observation of the figures available (Števčić, 1993) reveals many morphological similarities between *Trichopeltarion* and *Krunopeltarion*. The outline, described as subcircular, but not entirely figured, would resemble that of several species of *Trichopeltarion*. The tridentate rostrum and morphology of the three orbital spines is also like that of *Trichopeltarion*. The long slender retractable eyes, antennae and antennule morphology are also similar to *Trichopeltarion*. The lateral spines are almost identical to that of *T. nobile* and *T. greggi*. Although the exact ornamentation type cannot be observed from the figure, the spacing and arrangement of tubercles on regions can also be observed in *Trichopeltarion*. The

single most important, and possibly only, character that separates *Krunopeltarion* from *Trichopeltarion* is that the sternal suture six/seven is incomplete whereas it is complete in specimens of *Trichopeltarion*.

The other characters used by Števčić to distinguish *Krunopeltarion* from *Trichopeltarion* are actually species-level characters or are merely uninformative. Difference of tubercle type is a species level character. The lateral teeth being compound and triangular at the base is observed in several species of *Trichopeltarion*. Therefore it is not a character that distinguishes *Krunopeltarion* from *Trichopeltarion*. The distinct furrows on the surface of the carapace described by Števčić may be present on other atelecyclids, notably *Trichopeltarion* which has furrows created by the large swellings of regions. However, the furrows described by Števčić (1993) are not illustrated, making a comparison difficult. The sternal incomplete suture six/seven is a character that by itself distinguishes *Krunopeltarion* from the other atelecyclids.

Other Genera

Family CHEIRAGONIDAE Ortmann, 1893

Genus *TELMESSUS* White, 1846

Cancer TILESII, 1812 (1815), p. 347, Pl. 7, fig. 1.

Cheiragone? LATREILLE, 1825, p. 270.

Cheiragonus? BERTHOLD, 1827, p. 256.

Telmessus WHITE, 1846, p. 497; BENEDICT, 1892, p. 223;

SCHMITT, 1921, p. 235; RATHBUN, 1930b, p. 150, fig. 21;

URITA, 1936, p. 69–88; SAKAI, 1939, p. 434; SAKAI, 1976, p. 314–315; HART, 1982, p. 204–205.

Platycorystes BRANDT, 1848, p. 179.

Cheiragonus BRANDT, 1851, p. 147.

For additional information see Rathbun (1930b).

Type species

Cancer cheiragonus Tilesius, 1812 (1815).

Diagnosis

Carapace broader than long, strongly pentagonal. Lateral margins dentate with compound teeth. Front projecting between antennae, anterior edge cut into four small teeth. Broad tooth at inner angle of orbit. Basal article of antenna short, broad and flattened; a triangular winglike projection from basal article fills inner hiatus of orbit. Epistome with triangular point extending forward on median line between antennules. Chelipeds short; ambulatory legs moderately long. Sternum of female thickened and sculptured around genital openings; lateral margins of sixth abdominal segment broadly incised leaving openings fully exposed. Abdomen of male narrow, triangular from fourth segment to tip. (Modified from Rathbun, 1930b, p. 150–152.)

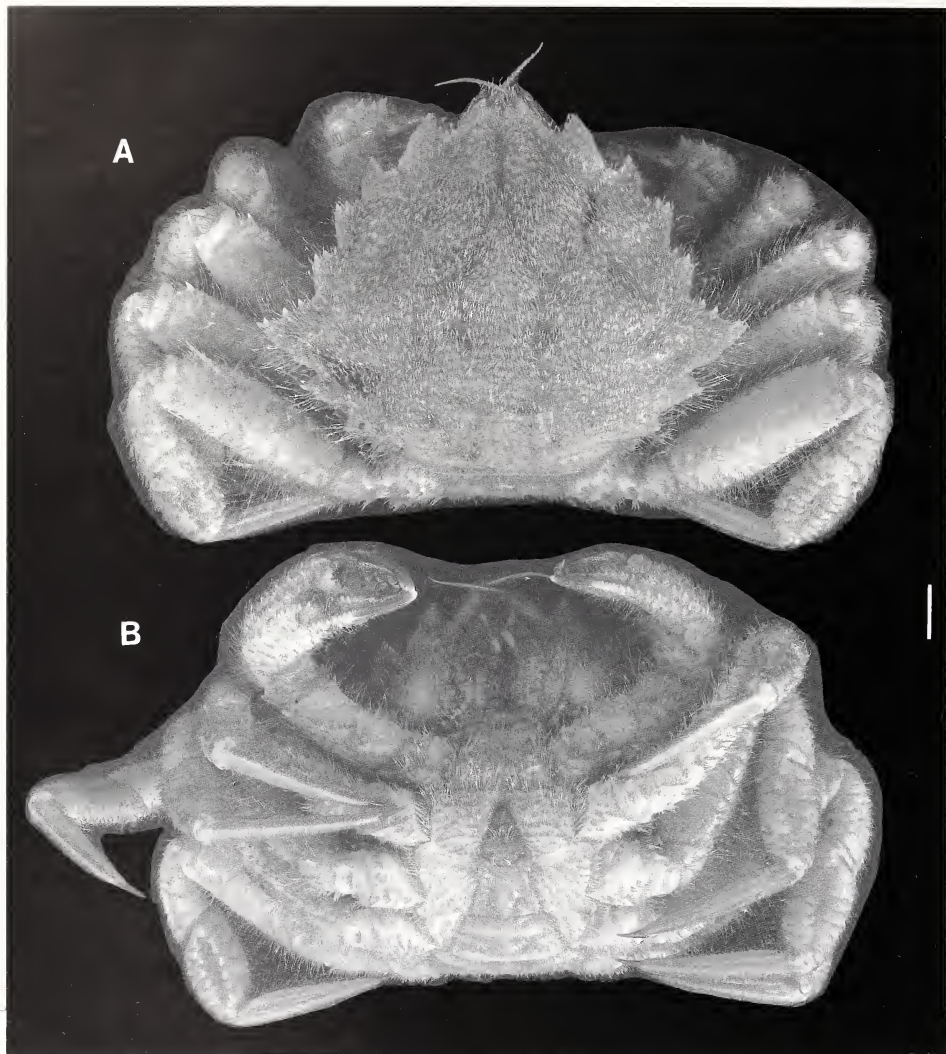


Figure 32. *Telmessus cheiragonus*, USNM 47963. Dorsal (A) and ventral (B) views. Scale bar equals 1 cm.

TELMESSUS CHEIRAGONUS (Tilesius, 1812 (1815))

Figure 32

Cancer cheiragonus TILESIIUS, 1812 (1815), p. 347.

Telmessus serratus WHITE, 1846, p. 497.

Platycorystes ambiguus BRANDT, 1848, p. 179.

Platycorystes cheiragonus BRANDT, 1851, p. 85.
Cheiragonus hippocarcinoides BRANDT, 1851, p. 147.
Cheiragonus cheiragonus ORTMANN, 1894, p. 420.
Telmessus cheiragonus HOLMES, 1900, p. 69; HART, 1982, p. 204–205. For additional synonyms of *T. cheiragonus* see Sakai (1976, p. 314).

Occurrence

Sand or mud substrates. Usually subtidal, on sandy or muddy tideflats, among eelgrass or algae. During breeding season, in early spring, they may be found intertidally on rocks covered with algae. Intertidal to 110 m (Hart, 1982, p. 204).

Distribution

From northern California to Bering Sea and southward from Siberia to Japan (Rathbun, 1930b, p. 152–155).

TELMESSUS ACUTIDENS (Stimpson, 1858)

Cheiragonus acutidens STIMPSON, 1858, p. 40.
Telmessus acutidens MIERS, 1879, p. 36.
Cheiragonus cheiragonus ORTMANN, 1894, p. 420.
Telmessus cheiragonus BALSS, 1922, p. 98; YOKOYA, 1928, p. 771; SAKAI, 1935, p. 140, fig. 66. For additional synonyms see Sakai, 1976, p. 315.

Occurrence

Bottoms of sand or mud; littoral to 50 m deep (Sakai, 1976, p. 315).

Distribution

On the Pacific side of Japan. Species ranges from Muroran, Hokkaido southward to Tokyo Bay; on the continental side, it ranges from the west coast of Hokkaido and south of Sakhalin southward to Korea Channel (Sakai, 1976, p. 315).

Remarks

This species appears to be endemic to Japan.

Genus *ERIMACRUS* Benedict, 1892

Type species

Platycorystes (Podacanthus) isenbeckii Brandt, 1848 = *Erimacrus isenbeckii* Benedict, 1892.

Diagnosis

Carapace longer than broad, elongate oval. Lateral margins arcuate, armed with seven teeth. Front between antennae with two teeth. A tooth at inner angle of orbit. Antennae as in *Telmessus*. Epistome with a nearly straight anterior margin. Chelipeds stout; ambulatory legs very broad and spinous. Genital openings of female occupy posterior wall of deep depression in sternum and not covered by abdomen.

Side margins of sixth segment of abdomen not deeply incised. Abdomen of male triangular from third segment. (Modified from Rathbun, 1930b, p. 155.)

ERIMACRUS ISENBECKII (Brandt, 1848)

Figure 33

Platycorystes (Podacanthus) isenbeckii BRANDT, 1848, p. 180.
Platycorystes isenbeckii BRANDT, 1851, p. 83.
Cheiragonus isenbeckii BRANDT, 1851, p. 147.
Erimacrus isenbeckii BENEDICT, 1892, p. 229, Pl. 26, figs. 5–7, and Pl. 27.

Occurrence

Bottoms of sand, mud, gravel or broken shell at depths from 10 to 200 m (Sakai, 1976, p. 316).

Distribution

From Cook Inlet, Alaska, westward and northward to the Pribilof Islands (Bering Sea) and Kamchatka, southward to Korea and southern Japan (Rathbun, 1930b). For additional locality information see Rathbun (1930b, p. 158–159).

Genus *MONTEZUMELLA* Rathbun, 1930

Remarks

Montezumella tabulata Rathbun was believed to be an atelecyclid (Rathbun 1930a). The fossil material does show some apparent morphological similarities with other atelecyclids. The supraorbital spines and ornamentation of the carapace are atelecyclid characters. However, the deep furrows that delineate regions do not seem to be the same as in atelecyclids. Also, the rostrum has not been described making the observation of a tridentate front impossible.

The genus has been placed within the Cheiragonidae by Schweitzer and Salva (2000). The anterolateral spines, if present, are worn away, as are the possible lateral spines. While characters suggest the possible placement of *Montezumella* in the atelecyclids, the lack of a complete, or near complete, set of defining characters does not allow its placement within the Atelecyclidae.

Family MAJIDAE Samouelle, 1819

Genus *PLIOSOMA* Stimpson, 1860

Type species

Pliosoma pavifrons Stimpson, 1860 (Figure 14).

Diagnosis

Carapace longer than broad, pear-shaped. Orbits comprised of a series of spines, directed forward. Chelipeds and first two legs long and slender. Last two legs subnatatory. Modified from Rathbun (1930b, p. 169).

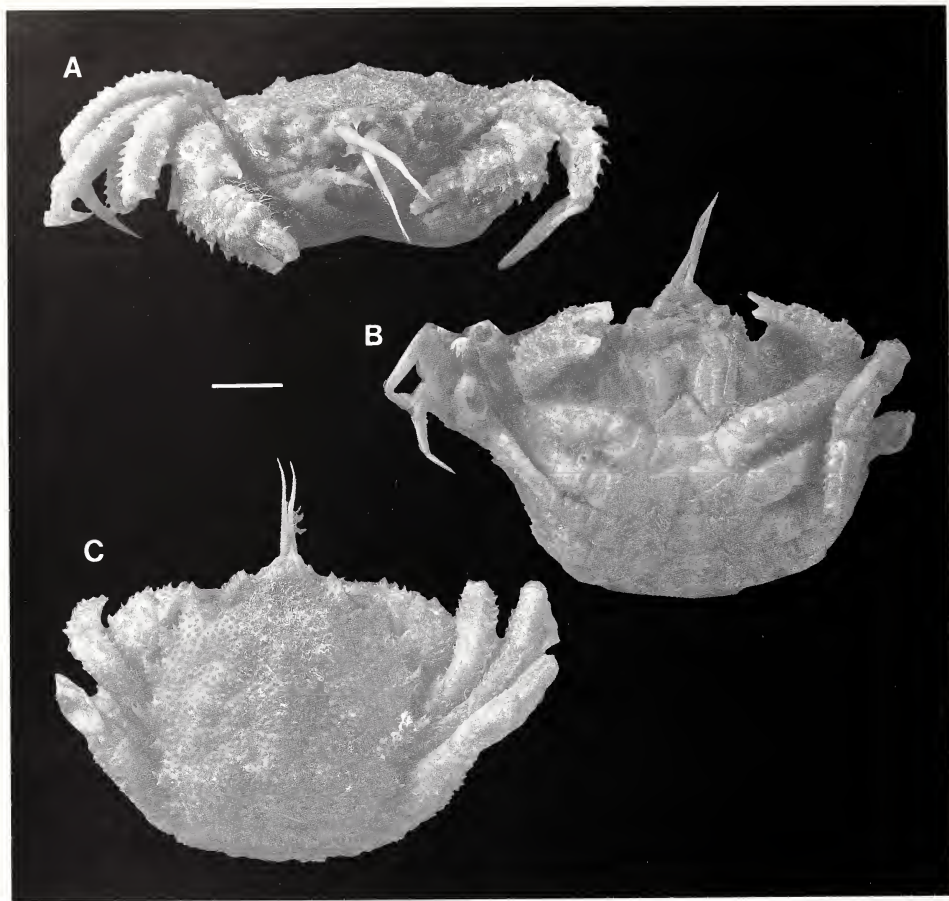


Figure 33. *Erimacrus isenbeckii*, USNM 54483. Orbital (A), ventral (B), and dorsal (C) views. Scale bar equals 1 cm.

Distribution

Cape San Lucas, Baja California, Mexico; ?Carmen Island (Rathbun, 1930b, p. 170).

Remarks

Until the observations of Guinot (1979, p. 257), the genus *Pliosoma* had been assigned to the Atelecyclidae. Stimpson first assigned *Pliosoma* to the Atelecyclidae, and this was followed by Rathbun (1930b, p. 169) and Balss (1957, p. 1635). The genus was attributed to the Majidae by

Guinot (1979). Characters supporting this assignment are as follows: The sternal sutures, four/five through seven/eight are incomplete as in the Majidae. Also the first pleopod of the male is characteristic of the majids. The chelipeds are not much longer than the second and third pereopods. The second article of the antenna is well developed. The orbits are more or less incomplete. General observations indicate that *Pliosoma* possesses a pear-shaped carapace that is common in many majids, and a broadened star-shaped sternum as in *Leurocyclus* Rathbun, 1897.

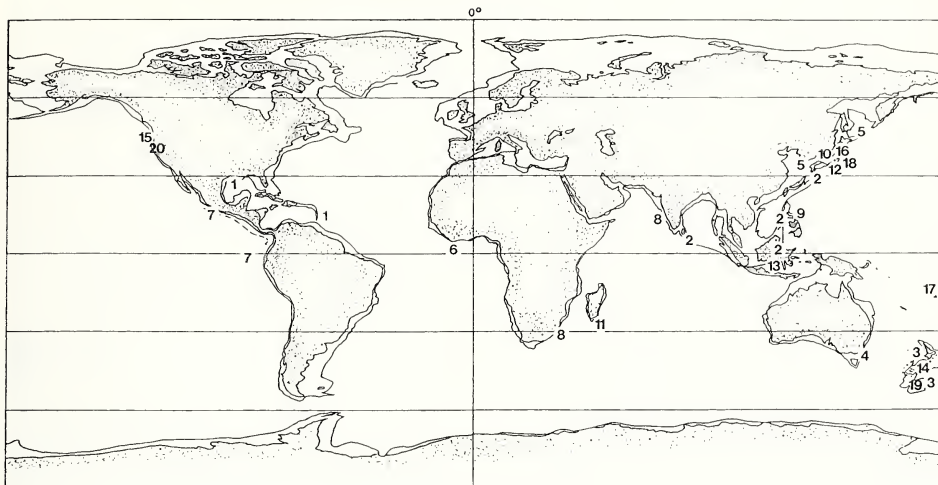


Figure 34. Distribution of *Trichopeltarion* species. (1) *T. nobile*; (2—) *T. ovale*; (3) *T. fantasticum*; (4) *T. wardi*; (5) *T. balssi*; (6) *T. intensi*; (7—) *T. corallinus*; (8) *T. glaucus*; (9) *T. alcocki*; (10) *T. elegans*; (11) *T. crosneri*; (12) *T. sagamiensis*; (13) *T. moosai*; (14) *T. greggi*; (15) *T. berglandorum*; (16) *T. huziokai*; (17) *T. decorus*; (18) *T. inflatus*; (19) *T. merrinae*; (20) *T. granulosa*. The solid lines and the dashed lines connect similar numbers and denote a geographic range of the taxon, rather than a single site of occurrence.

We suggest tentative assignment into the majid subfamily Pisinae, based upon the following characteristics from Griffin and Tranter (1986): The supraorbital cave is small and weakly developed with no preorbital spine. The postorbital process is prominent, and cupped to receive the eyestalk when retracted. Eyestalks are short. There is no intercalated spine. The basal article of the antenna is produced into a spine that forms the suborbital boundary.

Family ?CANCRIDAE Latreille, 1803

Genus *CYCLOCANCER* Beurlen, 1958

Remarks

Beurlen established the genus based upon *Cyclocancer tuberculatus* from the Miocene of Brazil. The genus was proposed as a transition between *Cancer* and *Atelecycylus*. The figure of the moderately well-preserved specimen (Beurlen, 1958, Pl. I, fig. 6.) of *Cyclocancer* is much wider than long. On this character alone, *Cyclocancer* does not conform to the revised definition of the Atelecyclidae, but appears closer to the Cancridae. However, to properly identify defining characters, the type specimen would be needed. Beurlen's (1958) proposal that *Cyclocancer* is transitional between *Cancer* and *Atelecycylus* would suggest that it exhibits characters that would make its placement into either of the respective families questionable. If *Cyclocancer* is

indeed transitional between the two type genera, then it should belong in a distinct family. *Cyclocancer szontaghi* has been synonymized with *Atelecycylus szontaghi* and placed into the genus *Tasadia carniolica* (Bittner, 1884) by Janssen and Müller, 1984.

Family DAKOTICANCRIDAE Rathbun, 1917

Genus *AVITELMESSUS* Rathbun, 1923

Type species

Avitelmessus grapsoides Rathbun, 1923.

Remarks

The genus *Avitelmessus* was first established as an atelecyclid by Rathbun (1923), but has since been reassigned to the Dakoticancridae by Glaessner (1960, p. 46). There are several characters possessed by *Avitelmessus* that do not conform to the expanded definition of the Atelecyclidae. The body shape is oblong-ovoid, and wider than long. The front is not cut into three or four teeth. The anterolateral margins do not possess compound teeth. The sternum is broad, not elongate ovoid as in typical atelecyclids.

Conclusions

A systematic and cladistic study of the Atelecyclidae has led to a new and expanded definition of the family. The

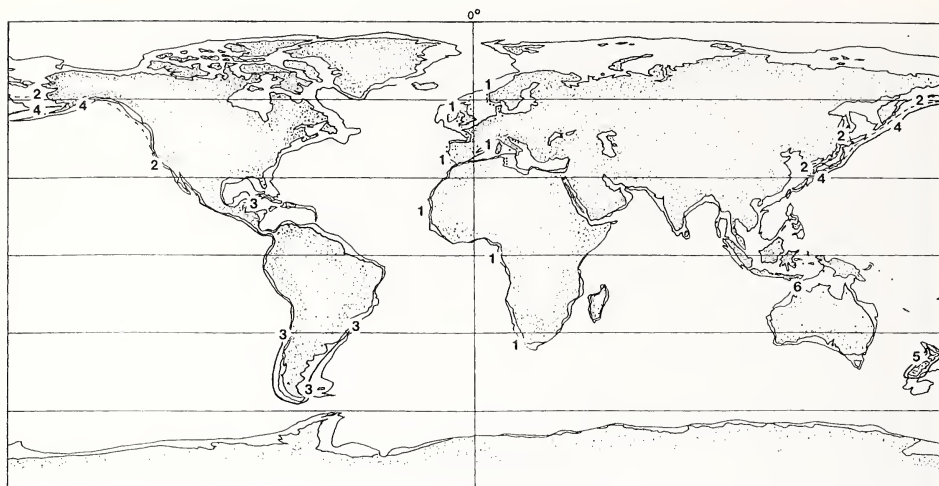


Figure 35. Distribution of genera within Atelecyclidae, excluding *Trichopeltarion*. (1) *Atelecyclus*; (2---) *Telmessus*; (3—) *Peltarion*; (4—) *Erimacrus*; (5—) *Pteropeltarion*; (6) *Krumpholtarion*.

cladistic analysis of the family on the generic level defines probable phylogenetic relationships between the genera, reinforces classifications based upon systematic observations, and supports referral of several genera, previously placed in the family, to other families. The long-standing problem of differentiating *Trichopeltarion* from *Trachycarcinus* was resolved by redefining the genus; the two genera were synonymized into *Trichopeltarion*. The wide range of variation among species within the two previously established genera provided a basis for the synonymization, along with the recognition that paedomorphic events, namely progenesis, explain many morphological differences between species within the genus *Trichopeltarion*. We have assigned genera thought at some time in the past to belong to the Atelecyclidae to the appropriate families of Atelecyclidae, Cheiragonidae, Belliidae, Thiidae, Majidae, and Dakoticancridae where possible.

The distribution of the genus *Trichopeltarion* proves to be quite disjunct (Figure 34). All but three of the species are found in the Indo-Pacific. The type species, *T. nobile*, is found in the Gulf of Mexico and the Caribbean; *T. corallinus* ranges from Acapulco to the Galapagos Islands; and *T. intensi*, which has been retained in the genus without observation of a specimen or photo, is known from one locality, Ivory Coast, Africa. The other genera within the family are strongly concentrated in the Indo-Pacific (Figure 35). All of the genera have ranges that include the Pacific, except the type genus *Atelecyclus*, which ranges from Scandinavia to South Africa in the Eastern Atlantic Ocean.

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KIRTLANDIA®

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PRESENTATION OF THE DAVID S. INGALLS, JR. AWARD FOR EXCELLENCE*

PRESENTATION OF THE AWARD

MIRIAM G. SMEAD

Trustee, The Cleveland Museum of Natural History
1 Wade Oval Drive, University Circle
Cleveland, Ohio 44106-1767

Tonight The Cleveland Museum of Natural History has the honor of presenting the sixth David S. Ingalls, Jr. Award for Excellence. It is awarded to an individual for excellence in research, education, or conservation in one of the fields of natural science represented by the Museum. Our honoree is Dr. Tim D. White, who, at the age of 50, has become a major figure in human evolutionary studies. Dr. White is our youngest recipient of this prestigious award.

His academic training began at the University of California, Riverside where he received his Bachelor of Science degree in biology and anthropology. Just last year that university honored him with their Distinguished Alumnus of the Year Award. He earned his master's and doctoral degrees at the University of Michigan in Ann Arbor in the field of biological anthropology.

He is presently a professor in the Department of Integrative Biology at the University of California, Berkeley. Concurrently, he is the Curator of the Physical Anthropology collection at the Hearst Museum.

Professor White has made enormous contributions to the field of human evolution. He is internationally recognized as the leading expert on hominid evolution during the Pliocene. He has been part of the team that discovered and named one genus, *Ardipithecus*, and three species,

Ardipithecus ramidus, *Australopithecus afarensis*, and *Australopithecus garhi*, of early hominids. No other single individual has accomplished this feat.

Dr. White's African research in the field of paleontology began at Lake Turkana in Kenya in 1974. It then expanded into the famous sites of Laetoli and Olduvai Gorge, Tanzania. Later his efforts centered on the Main Rift Valley and Afar regions of Ethiopia. For the past twenty years he has been a paleoanthropology team leader in the Middle Awash Research area of Ethiopia. Admirably, in his work there, he has trained a number of African Ph.D.s.

During the quarter of a century he has carried on fieldwork in eastern and southern Africa he has been responsible for the discovery of dozens of new fossil localities. Dr. White developed the excavation method used at the famous Laetoli footprint locality. He was also largely responsible for equipping and organizing the physical anthropology laboratory at the National Museum of Ethiopia. It is here that the fossil bones of Lucy are now safely preserved, for after five years of scientific study and the production of casts of the bones here at The Cleveland Museum of Natural History, the fossils were returned to their country of origin. Dr. White was a primary player in the study of Lucy.

* On March 9, 2001, the David S. Ingalls, Jr. Award for Excellence was presented to Tim D. White. The remarks printed here are excerpted from those presented on that occasion.

For over twenty years he has been affiliated with The Cleveland Museum of Natural History as a Research Associate in Physical Anthropology. He has done extensive study of our world renowned Hamann-Todd Skeletal Collection and worked with Museum staff to develop the techniques used to replicate the Ethiopian Fossils. In 1978 he coauthored a key scientific paper with Dr. Yves Coppens and Dr. Donald C. Johanson, who was at that time our Curator of Physical Anthropology. This research paper, introducing the Lucy fossils to the world, was entitled "A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa." It was published in the Museum's scientific publication, *Kirtlandia*.

In addition to his work in Africa, Dr. White's research has taken him worldwide. He has studied fossil remains of hominids and other fauna in Asia, the Middle East, and Europe. His research has included extensive study of human and non-human primate skeletal collections at museums in our country and many countries abroad. Funding for his research on the origins of man has come from numerous grants provided by organizations such as the National Science Foundation, the National Geographic Society, and The L. S. B. Leakey Foundation.

Dr. White has over 100 publications, including three books, to his credit. His *Human Osteology* (2000), is the leading textbook on the study of the human skeleton. He is the world's authority on cannibalism and wrote the leading book on that topic in 1992. He is also a world authority on fossil pig evolution and published the leading monograph on that subject in 1979.

Is it any wonder that his work has appeared on the covers of the journals *Nature* and *Science* several times? This is surely indicative of his stature in the scientific community.

With his extensive knowledge of human evolution, he has often written reviews of books by others in his field. He has presented professional papers at scientific conferences here and abroad and has been an invited lecturer at universities, colleges, museums, and other institutions worldwide. Also, he has received numerous prestigious scientific awards.



Tim D. White, March 9, 2001

Dr. White, your influence on the field of physical anthropology is immeasurable. Your research has been of tremendous benefit to the enlightenment of humankind in understanding our genesis and evolutionary history. It is truly an honor for me, on behalf of the Board of Trustees of The Cleveland Museum of Natural History, to present this award to you in recognition of such excellence in your chosen field.

REPLY

TIM D. WHITE

Laboratory for Human Evolutionary Studies
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A few years ago, the American Academy of Achievement made a film about scientists and how they were drawn to science. Featured were the giants of physics, chemistry, molecular biology—scientists whose names are familiar to us all. And it turns out that a remarkable number of these luminaries began their scientific investigations of the world with early experiences in natural history.

Natural history served them, and serves us today, as a critically important portal through which young people engage and enter science. This wonderful museum, with its world-class research, its superb collections, and its cutting-edge educational programs, is contributing enormously to Ohio, the nation, and the world. The world of science will continue to owe a great debt to institutions such as this one—crucibles that help foster the development of good science.

There will always be a place for great museums of natural history, and it is a personal delight for me to return here to accept the David S. Ingalls, Jr. Award for Excellence. I am particularly touched by the wonderful sculpture that Larry Isard has made for this occasion, a work of art that truly captures the essence of the majestic gorilla and will always remind me of tonight.

I first came here as a graduate student, and I've come back many times in the last 27 years. This lecture is associated with an award, but I cannot accept this as an award to Tim White. You see, by definition, any award bestowed on me rewards the efforts and contributions of the team of people I work with. I can therefore only accept this award on behalf of all of my colleagues. Several team members are here tonight. Professor C. Owen Lovejoy, from Kent State University is here. How many times have Owen and I gone back to the collections downstairs to check another observation, to gain another insight? And Bruce Latimer, now in charge of Physical Anthropology at the museum. Bruce is always a source of inspiration, with a smile and character that energize all around him, here and also in the deserts of Africa. And Scott Simpson, who's not here at the moment, but who is right now probably watching the sun rise in Ethiopia, hopefully on his way to finding another hominid. And Luba Gudž, an artist here at the museum who has accurately rendered our discoveries for a worldwide audience of scientists over the last quarter of a century. And Lyman Jellema.

Nobody knows the collections like Lyman. No other person has figured so importantly, in so many research efforts in physical anthropology, by so many colleagues around the world, as Lyman. It is indeed a great honor and a warm feeling to be among such friends and colleagues tonight.

Research in Africa shows that we weren't always humans. And we weren't EVER chimpanzees. Work like that conducted by the large group of people I have mentioned is the only means to approach the deep past and to extract clues that can teach us about it. Tonight I speak for all these colleagues on the Middle Awash research project, colleagues who study everything from the interpretation of satellite imagery to the biomechanical analysis of the recovered fossils, from the isotopic studies of the rock and soil samples to the shapes and sizes of lizards and birds and bats and snails, and so many other clues that have managed to escape the ravages of time. All of this work is aimed at revealing the ways that we were.

The creationist prediction about what all this research would reveal is simple. For the creationist, it was all modern humans, all the way back. Darwin's prediction was different. Today, the Middle Awash affords us a great open-air laboratory in which to directly test these very different predictions.

Any one of about eight slices thru time that we are currently investigating in the Middle Awash project would be a lecture in itself. Tonight I've chosen to focus on the way we were two-and-a-half million years ago, and to concentrate on a behavioral revolution in the human career.

We have discovered a new species of *Australopithecus* that we have named *garhi*, the Afar word for "surprise," because of its surprising combination of features, and because it was found in a horizon where the butchery of large ungulates with stone tools had occurred two-and-a-half million years ago. These discoveries have opened a window on a poorly-known period in Africa, further illuminating our ancestry.

Lacking a fossil record for the human past, Darwin was forced to triangulate ancestors from evolution's end products—modern people and modern apes. He concluded that our evolution involved a gradually expanding brain, reducing canine teeth, increasing bipedality, and tool use. We now know that we didn't happen that way.

By at least four million years ago, there were fully bipedal creatures with small canines and small brains and no stone tools. Much later, by 2.5 million years ago, we now know that stone tools and large mammal butchery were key parts of one hominid's behavior. By two million years ago, larger-brained bipeds had appeared.

The new discoveries of early hominids and their behaviors tell us that some time shortly after three million years ago a bipedal primate embarked on a technological journey that would ultimately take it to the Silicon Valley, and on into space.

Going "lithic" at 2.5 million years ago was a big revolution—it expanded the small brained bipedal primate's niche to make it a super-omnivore. Here was a primate that directly competed with hyaenas, wild dogs, and large cats. This revolution had vast implications for selective pressures on this primate, and, ultimately, on its descendant's geographic spread out of Africa.

This behavioral revolution was probably the second largest behavioral shift in our career, second only to the evolution of bipedality that we now know to have come millions of years earlier.

In this field, people go on and on about the names of fossils. And about their different ideas regarding the shape details of the family tree. The bottom line is that the detailed geometry of this tree is still unknown because there's not enough evidence. Only work in the fossil fields and in developmental biology laboratories will bring us closer to resolving issues of early hominid species and their relationships.

But the variety of tongue-twisting names and the rapidly-changing family trees are not interesting compared to the big picture. What's the big picture that's already been sketched in by paleoanthropology? As Darwin predicted, the record clearly shows increasingly apelike hominids the further back you go.

And T. H. Huxley's as right as he was over a century ago. This search for our origins is still the most fascinating of all human investigations. Human evolutionary studies present fundamentally interesting questions. The creationist answers developed a few thousand years ago by hunter-gatherers in Australia, by farmers in Mesoamerica, and by prehistoric pastoralists in the Middle East, are all interesting and important—but in a folkloric perspective, and in the context of religious studies, NONE of these myths have predicted what we have ALREADY found in the Middle Awash.

There are many more things to learn, but here in ONE place in the Horn of Africa, in the Middle Awash, we have a sequence that already shows what some people don't want the kids in Kansas to know: Our African roots are very deep, and it wasn't humans all the way back.

So that's my report about what we've been learning about the way we were at 2.5 million years ago. I hope that Owen, and Bruce, and Scott, and I will have more chances to get together with you here as the leadership, staff, and collections of The Cleveland Museum of Natural History continue to support our research, and as we continue to publish some of the other things that we've found in Ethiopia—fossils and their contexts that tell us about the ways we were at a quarter million, one million, 4.4 million, and now even 5.8 million years ago.

This museum has played a major role in these discoveries, and in the building of knowledge about our ancestry. I am both proud and humbled to have been a participant in this research, and along the way to have explored the wonderful collections held in trust at an institution with such a glorious past and a bright, beckoning future. I thank you for inviting me, and for this wonderful award.

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FRANCES B. KING

The Cleveland Museum of Natural History
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Introduction

Kirtlandia was first published in 1967. The inaugural paper by James L. Murphy and Larry Picking was on the geology and paleontology of a new marine member of the Conemaugh Group, a series of fossil-bearing units that occur in Ohio and adjacent West Virginia and Pennsylvania. This was the first of numerous papers dealing with the paleontology of the midwestern United States, one of the main interests of The Cleveland Museum of Natural History. Many species of fossil animals from this and other areas have been formally named in the journal by Museum scientists and others in the scientific community. Archaeology is also well represented in the journal, which has included reports on a series of prehis-

toric sites excavated by museum archaeologists. Other disciplines represented in the journal include botany, paleobotany, physical anthropology, zoology, and ecology.

This index covers the issues of the journal published during its first thirty-five years (1967-2001). It is comprised of three parts: an author index, a title index, and a subject index. Square brackets [] are used in some cases to indicate elucidations.

Acknowledgments

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Supported by the Kirtlandia Society of The Cleveland Museum of Natural History, *Kirtlandia* is devoted to the publication of scientific papers in the various fields of inquiry within the Museum's sphere of interest: Cultural and Physical Anthropology; Archaeology; Botany; Geology; Paleobotany; Invertebrate and Vertebrate Paleontology; Systematics; Ecology; and Invertebrate and Vertebrate Zoology. Issues will vary from single monographs to collections of short papers, review articles, and brief research notes.

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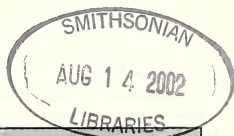
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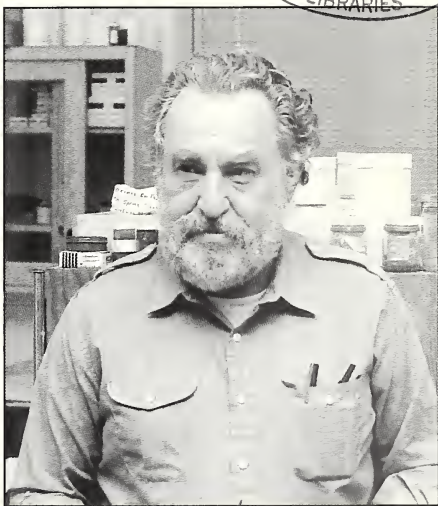
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DEDICATION TO BARRY B. MILLER



This issue of *Kirtlandia*, the scientific publication of The Cleveland Museum of Natural History, is dedicated to Dr. Barry B. Miller, emeritus professor of geology at Kent State University and a nationally prominent Pleistocene paleoecologist and malacologist. This dedication honors his contributions to the study of the paleontology and paleoecology of Late Cenozoic deposits of North America, particularly north-eastern Ohio, the Great Plains, and the Great Lakes region.

Barry was born and grew up in the Bronx, New York City. He loved aspects of New York, but was not really a big city person. Barry took a night course in geology at City College while working full-time in New York. It was his plan to leave New York and go into forestry, and the geology course was one of the requirements for a forestry degree. He left New York and attended the Michigan College of Mining and Technology in Houghton, receiving a certificate in forest industries. He then went to the University of Michigan at Ann Arbor, and after his first semester, took a job in forestry, watching for fires in a fire tower. The utter loneliness of sitting in a fire tower destroyed his interest in forestry as a career. He changed fields to geology and completed undergraduate (B.S., 1958) and graduate work (M.S., 1960; Ph.D., 1963) in geology at the University of Michigan. There he became immersed in the paleontological and malacological milieu of the University of Michigan Museum. He worked under the direction of, and alongside, Claude W. Hibbard (1905-1973), participating in a number of trips to Kansas and Oklahoma led by the legendary University of Michigan vertebrate paleontologist. Barry focused his energy on molluscs collected during these expeditions. He published his first paper (Miller, 1961) on Pleistocene molluscs from Kansas. In later years, Barry would regale his students with tales of work in the field with Hibbard, a man who disdained modern conveniences during field expeditions. Hibbard, for example, would not permit the use of an ice box for food storage because it required going to town several times during the week to replenish the ice supply, which would reduce the amount of time that could be spent doing field work. Barry's Ph.D. dissertation was on molluscan faunas of the southern Great Plains. It was published (Miller, 1966) in the journal *Malacologia*.



Barry came to Kent State University as an assistant professor in 1963 and was promoted to a full professor in 1977. He also taught geology for a time at the University of Akron. At KSU, Barry helped to develop a series of student lab manuals (e.g., Miller and Feldmann, 1968a), and an innovative plan that would have used the campus as a field site for an introductory mapping exercise (Miller and Feldmann, 1968b). Barry taught a number of courses over the years. These included historical geology, glacial geology, Pleistocene stratigraphy and chronology, systematic invertebrate paleontology, geology of Ohio, introductory geology, and a seminar in paleoclimatology. As a professor, Barry stood out because of his colorful language. He was also notable for being generous with time for students, even students working under the guidance of other professors. He was, however, a demanding professor, who expected his students to hold to high standards of scholarship.

Barry used *Glacial and Quaternary Geology* by R. F. Flint (1971) as the text for his glacial geology classes. His own investigations were to eventually cover many of the topics included in Flint's classic book. Over a period of several decades, Barry investigated many of the textbook topics, adding new insights into our view of the Late Cenozoic. He also helped to energize investigations of this time period by the use of technology. With a series of colleagues, mostly from the United States and Canada, he applied radiocarbon dating (Farrand and Miller, 1968), amino acid racemization (Miller et al., 1987), and oxygen isotopes (Miller et al., 2000) to projects. Barry's focus remained, however, on molluscs, especially on snails as paleoenvironmental indicators (Miller et al., 2002). He and his colleagues used molluscs (especially snails) and other information, to document events in the history of the Great Lakes (Miller et al., 1985) and elsewhere (e.g., Li et al., 1998; Miller et al., 1994; Miller et al., 1979).

A true "friend of the Pleistocene," Barry attended and contributed (e.g., Paulson et al., 1990) to the Friends of Pleistocene's field trips in various parts of North America. He also contributed to the field by authoring papers on methods (Miller, 1989; Miller and Bajc, 1989).

Barry has authored or coauthored a number of works on the glacial geology of northeastern Ohio over a span of three decades. These have included an overview of the glacial geology (Miller, 1970) of the region, articles dealing with the now classic (in part because of his work) Garfield Heights localities (e.g., Miller and Wittine, 1972; Miller and Szabo, 1987), and an investigation of the stratigraphy at the Southerly Wastewater Treatment Plant (Miller, 1983) in the Cuyahoga Valley. Barry has also investigated the peat deposits of northeastern Ohio (Miller et al., 1984).

As the list of references below indicates, Barry has collaborated with many people over the past few decades, including a number of geologists on the staff of Kent State and other northeastern Ohio universities. Two of us (Rod Feldmann and Michael Tevesz) have been fortunate enough to have been included among these collaborators. Barry has also been willing to contribute chapters to books that we have edited. Among these are chapters on gastropods and pelecypods (Hoare and Miller, 1996a, 1996b) in *Fossils of Ohio*. Rod worked with Barry since they first met as young assistant professors at KSU. These colleagues shared side-by-side offices for most of that time and both taught courses in the same upper division paleontology sequence. Mike began working with Barry after a meeting with Joe Hannibal in The Cleveland Museum of Natural History. When Mike mentioned that he was doing stable isotope work on mollusc carbonate and had an interest in Holocene paleolimnology, Joe suggested that he contact Barry and talk about the possibility of working together. Thus began a long and productive collaboration focused on interpreting data from sediment cores in order to do paleoenvironmental and paleoclimatic reconstructions. Barry was always full of ideas, had some remarkable samples already collected, and was very generous about sharing both.

This issue of *Kirtlandia* contains an article (Miller et al., 2002) on Kansas land snails by Barry and his colleagues. This article grew out of his collaboration with Mike. There are also four articles dealing with molluscs of northeastern Ohio, and one nonmolluscan article on reidentification of a fossil plant as a millipede. The last article is coauthored by one of Barry's former students (Joe). We offer this collection as a modest tribute to Barry B. Miller, our dear colleague, teacher, and friend.

J. Hannibal, M. Tevesz, and R. Feldmann

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CLIMATIC GRADIENTS IN THE DISTRIBUTION OF KANSAS LAND SNAILS (MOLLUSCA: GASTROPODA)

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ABSTRACT

The distribution of 64 species of land snails (Mollusca: Gastropoda) across the 105 counties of the State of Kansas was analyzed by principal components analysis to determine the relationship between species occurrence and climatic factors. Significant biotic responses of species assemblages to climatic gradients in precipitation and in annual temperature were discovered. In particular, total species diversity is positively correlated with precipitation (annual or summer alone) across the counties of Kansas, and the distributions of major clusters of gastropod species were correlated with average annual temperature (or latitude).

Introduction

This paper presents an analysis of the relationships between the distribution of species assemblages of land snails (Mollusca: Gastropoda) across the counties of the State of Kansas and gradients of climatic variables across those counties. For the large, mid-continental state of Kansas in the years represented by our data, the average annual precipitation across the 105 geopolitical divisions (the counties) ranged from 15.82 to 41.68 inches, while the annual average

temperature range was 50.6 to 58.9 °F, and the average number of frost-free days varied between 154 and 198.

Because the State of Kansas shows pronounced geographic clines in climatic conditions, our aim was to explore whether there is a faunal response to these gradients in a group of organisms likely to be dependent upon climatic factors. In a similar geographic study, Kadmon and Heller (1998) found a strong correlation between species distributions of land snails in Israel and the climatic gradients found there.

Materials and Methods

The most recent published survey of species of land snails in Kansas remains the monograph of Leonard (1959), which gives distribution maps for each snail species in the counties of the state. Table 1 lists the 64 gastropod taxa found in Kansas, using nomenclature updated according to the systematic treatment of Turgeon et al. (1988) and earlier works (Pilsbry, 1948; Taylor, 1960; Taylor, 1965). The distribution maps were converted into a presence/absence data table, where each of the 105 counties was scored according to whether each of the species was recorded as present. The counties of Kansas were coded according to a letter-and-number checkerboard scheme (Figure 1), with lower letters of the alphabet to the east and higher numbers to the north. Thus, the most southeastern county (Cherokee) was coded A1, and the most northwestern county (Cheyenne) was coded O8.

Climatic data for the sample localities were taken from the nearest reporting station of the United States Weather Bureau for the period 1899–1938, corresponding to the majority of the collection dates for the specimens collected by Leonard (1959) for the Museum of Natural History at the University of Kansas. The five climatic parameters that were used correspond to average values for the main weather station in each county, using published maps (Kincer, 1941). Their descriptions are given in Table 2, along with latitude and longitude.

All statistical analyses were performed using the SPLUS 2000 software package (MathSoft, 1999). We used principal components analysis (Morrison, 1967; Gauch, 1982) to reduce the complexity of the distributions of the 64 species across the 105 counties in Kansas. This technique is commonly used in analyses of geographic distributions of biotic assemblages (Kadmon and Heller, 1998) to reduce the multivariate dimensionality of the original data. It constructs linear combinations of the original variables (in this case, the presences and absences of 64 species) that maximally encompass the variation in the original data. In particular, the first principal component accounts for the greatest variance in the species data; the second component is perpendicular to and uncorrelated with the first component, and it accounts for the second largest amount of variation; the third component is orthogonal to the first two and accounts for the next largest amount of variation; etc. These synthetic variables thus represent uncorrelated aspects of species distributions across the counties of Kansas.

The principal components for species distribution then were related to latitude, longitude, and the five specific climatic variables for the 105 counties by using simple linear regression and correlation techniques (Gauch, 1982; Sokal & Rohlf, 1995).

Results and Discussion

Principal components analysis of distributions of 64 gastropod species

Principal components analysis of the distributional data, based on the matrix of correlations among the 64 species variates, was successful in capturing a significant fraction of

O8	N8	L8	K8	J8	I8	H8	G8	F8	E8	D8	C8	B8	A8	
O7	N7	L7	K7	J7	I7	H7	G7	F7	E7	D7	C7	B7	A7	
O6	N6	L6	K6	J6	I6	H6	G6	F6	E6	D6	C6	B6	A6	
O4	N4	M4	L4	K4	J4	I4	H4	G4	F4	E4	D4	C4	B4	A4
O3	N3	M3	K3	J3	I3	H3	G3	F3	E3	D3	C3	B3	A3	
O2	N2	M2	L2	K2	J2	I2	H2	G2	E2	D2	C2	B2	A2	
O1	N1	M1	L1	K1	J1	I1	H1	G1	E1	D1	C1	B1	A1	

Figure 1. Map of the counties of Kansas, along with their letter-and-number codes, as follows: A1, Cherokee; A2, Crawford; A3, Bourbon; A4, Linn; A5, Miami; A6, Johnson; A7, Wyandotte; A8, Leavenworth; B1, Labette; B2, Neosho; B3, Allen; B4, Anderson; B5, Franklin; B6, Douglas; B7, Jefferson; B8, Atchison; B9, Doniphan; C1, Montgomery; C2, Wilson; C3, Woodson; C4, Coffey; C5, Osage; C6, Shawnee; C7, Jackson; C8, Brown; D1, Chautauqua; D2, Elk; D3, Greenwood; D4, Lyon; D5, Wabaunsee; D7, Pottawatomie; D8, Nemaha; E1, Riley; E2, Butler; E4, Chase; E5, Morris; E6, Geary; E7, Cowley; E8, Marshall; F4, Marion; F5, Dickinson; F7, Clay; F8, Washington; G1, Sumner; G2, Sedgwick; G3, Harvey; G4, McPherson; G5, Saline; G6, Ottawa; G7, Cloud; G8, Republic; H1, Harper; H2, Kingman; H3, Reno; H4, Rice; H5, Ellsworth; H6, Lincoln; H7, Mitchell; H8, Jewell; I1, Barber; I2, Pratt; I3, Stafford; I4, Barton; I6, Russell; I7, Osborne; I8, Smith; J1, Comanche; J2, Kiowa; J3, Edwards; J4, Pawnee; J5, Rush; J6, Ellis; J7, Rooks; J8, Phillips; K1, Clark; K2, Ford; K3, Hodgeman; K4, Ness; K6, Trego; K7, Graham; K8, Norton; L1, Meade; L2, Gray; L4, Lane; L6, Gove; L7, Sheridan; L8, Decatur; M1, Seward; M2, Haskell; M3, Finney; M4, Scott; N1, Stevens; N2, Grant; N3, Kearny; N4, Wichita; N6, Logan; N7, Thomas; N8, Rawlins; O1, Morton; O2, Stanton; O3, Hamilton; O4, Greeley; O6, Wallace; O7, Sherman; O8, Cheyenne.

the variation among all 105 counties in the first three principal components. Principal component 1, which accounted for 20.8 percent of the total variation in the data, loaded positively on all 64 species, except *Succinea pseudovava*, *Succinea vaginacontorta*, and *Gastrocopta cristata*; in other words, it contrasted the occurrences of these three species against those of the other 61 species, among which the highest loadings were attributed to *Zonitoides arboreus*, *Anguispira alternata*, *Philomycus carolinianus*, *Strobilops labyrinthicus*, *Gastrocopta armifera*, *Gastrocopta contracta*, and *Carychium exile*. The second principal component, accounting for another 11.2 percent of the variation, contrasted 19 species against the other 45. The third component comprised an additional 6.2 percent of the variation and contrasted the distributions of a different set of 30 species

Table 1. Systematics of the gastropod species (or subspecies) found in Kansas. The 28 species subset used in a second analysis described in the text is indicated with **boldface**.

Order	Family	Species	Order	Family	Species
Basommatophora	Carychiidae	<i>Carychium exiguum</i> (Say, 1822)	Punctidae	Pupillidae	<i>Punctum minutissimum</i> (L. Lea, 1841)
		<i>Carychium exile exile</i> I. Lea, 1842			<i>Gastrocopta armifera</i> (Say, 1821)
					<i>Gastrocopta contracta</i> (Say, 1822)
Stylommatophora	Bulimulidae		Succineidae		<i>Gastrocopta corticaria</i> (Say, 1816)
		<i>Bulimulus dealbatus dealbatus</i> (Say, 1821)			<i>Gastrocopta cristata</i> (Pilsbry & Vanatta, 1900)
	Cochlicopidae				<i>Gastrocopta holzingeri</i> (Sterki, 1889)
		<i>Cochlicopa lubrica lubrica</i> (Miller, 1774)			<i>Gastrocopta pellucida hordeacella</i> (Pfeiffer, 1841)
	Discidae				<i>Gastrocopta pentodon</i> (Say, 1821)
		<i>Anguispira alternata alternata</i> (Say, 1816)			<i>Gastrocopta procera procera</i> (Gould, 1840)
	Haplotrematidae				<i>Gastrocopta tappaniana</i> (C. B. Adams, 1842)
		<i>Haplotrema concavum</i> (Say, 1821)			<i>Pupoides albibras</i> (C. B. Adams, 1841)
	Helicarionidae				<i>Pupoides hordaceus</i> (Gabb, 1866)
		<i>Euconulus chersinus polygyratus</i> (Say, 1821)			<i>Pupoides inornatus</i> Vanatta, 1915
	Helicodiscidae				<i>Vertigo milium</i> (Gould, 1840)
		<i>Helicodiscus eigenmanni eigenmanni</i> (Pilsbry, 1900)			<i>Vertigo ovata ovata</i> Say, 1822
					<i>Vertigo tridentata</i> Wolf, 1870
		<i>Helicodiscus parallelus</i> (Say, 1817)			
					<i>Catinella vagans</i> (Pilsbry, 1900)
		<i>Helicodiscus singleyanus singleyanus</i> (Pilsbry, 1890)			<i>Catinella wandae</i> (Webb, 1953)
	Philomycidae				<i>Oxyloma retusum</i> (L. Lea, 1834)
		<i>Platimycus carolinianus</i> (Bosc, 1802)			<i>Succinea concordialis</i> Gould, 1848
	Polygyridae				<i>Succinea ovalis</i> Say, 1817
		<i>Allogona profunda</i> (Say, 1821)			<i>Succinea pseudavara</i> Webb, 1954
					<i>Succinea vaginacontorta</i> Lee, 1951
		<i>Euchemotrena leai aliciae</i> (A. Binney, 1841)			
					<i>Strobilops labyrinthicus</i> (Say, 1817)
		<i>Mesodon clausus</i> (Say, 1821)			
					<i>Deroceras laeve</i> (Müller, 1774)
		<i>Mesodon inflectus inflectus</i> (Say, 1821)			
					<i>Hawaii minuscula minuscula</i> (A. Binney, 1840)
		<i>Mesodon thyroideus thyroideus</i> (Say, 1816)			<i>Mesonplius cupreus ozarkensis</i> (Rafinesque, 1831)
					<i>Nesovitrea electrina</i> (Gould, 1841)
		<i>Polygyra dorfeuilliana dorfeuilliana</i> (L. Lea, 1838)			<i>Nesovitrea identata identata</i> (Say, 1823)
					<i>Paravitrea capsella capsella</i> (Gould, 1851)
		<i>Polygyra dorfeuilliana sampsoni</i> (L. Lea, 1838)			<i>Paravitrea significans</i> (Bland, 1866)
					<i>Paravitrea simpsoni</i> (Pilsbry, 1889)
		<i>Polygyra jacksoni jacksoni</i> (Bland, 1866)			<i>Striatura meridionalis</i> (Pilsbry & Ferriss, 1906)
					<i>Striatura milium</i> (E. S. Morse, 1859)
		<i>Stenotrema hirsutum hirsutum</i> (Say, 1817)			<i>Ventridens ligera</i> (Say, 1821)
					<i>Zonitoides arboreus</i> (Say, 1816)
		<i>Stenotrema stenotrema</i> (Pfeiffer, 1842)			
					<i>Vallonia parvula</i> Sterki, 1893
		<i>Triodopsis albolabris allenii</i> (Say, 1816)			
		<i>Triodopsis cragini</i> Call, 1886			
		<i>Triodopsis divesta</i> (Gould, 1848)			
		<i>Triodopsis multilineata algonquinensis</i> (Say, 1821)			
		<i>Triodopsis multilineata multilineata</i> (Say, 1821)			
		<i>Triodopsis neglecta</i> (Pilsbry, 1899)			

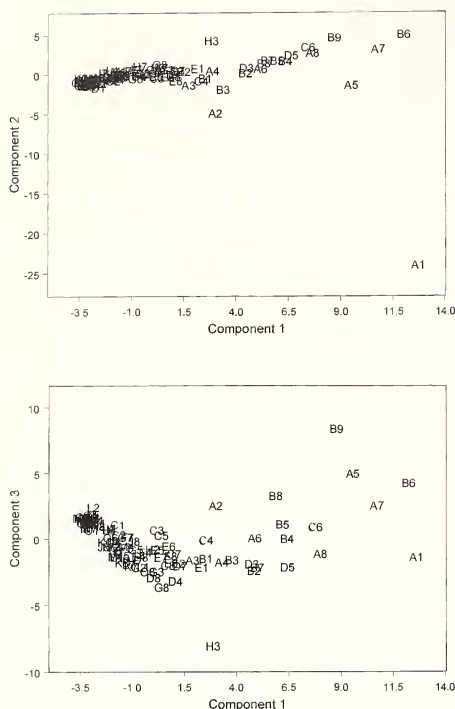


Figure 2. Location of the counties of Kansas (indicated with the locality codes of Figure 1) in the space defined by the first three principal components based on the distribution of 64 gastropod species.

against the remaining 34. Thus, the first three principal components together account for 38 percent of the variation in the distributional data of 64 gastropod species across the 105 counties of Kansas.

Inspection of the location of the individual counties in the three most important dimensions of principal components space (Figure 2) reveals that the most eastern counties of Kansas (codes A1 to D8) occur at the high end of the first principal component, that the most southeastern county (A1: Cherokee) is distinct with respect to the second principal component, and that there is some separation of the eastern counties, as well as H3 (Reno County) along the third component. The superposition of nearly all of the western counties indicate that they are distinct with respect to gastropod assemblages.

Table 2. The seven climatic variables and correlations of the first three principal components (comps.) of species distributions of 64 gastropod species with these climatic variables. The last five variables represent annual averages.

	Comp. 1	Comp. 2	Comp. 3
Latitude (°N)	0.151	0.303	-0.115
Longitude (°W)	-0.730	-0.040	0.099
Annual precipitation (inches)	0.730	0.010	-0.132
Summer precipitation (inches)	0.721	0.034	-0.150
Annual temperature (°F)	0.125	-0.203	-0.023
July temperature (°F)	-0.128	-0.091	-0.040
Number of frost-free days	0.436	0.157	0.013

Table 3. Correlations between principal component (comp.) scores based on 28 gastropod species and climatic variables in the counties of Kansas.

Species	Comp. 1	Comp. 2	Comp. 3
<i>Euchemotrema leai aliciae</i>	0.241	-0.136	0.001
<i>Mesodon thyridus thyridus</i>	0.139	-0.009	-0.332
<i>Mesodon clausus</i>	0.163	0.202	0.092
<i>Triodopsis albolabris alleni</i>	0.219	0.213	-0.073
<i>Bulimulus dealbatus dealbatus</i>	0.170	-0.122	-0.104
<i>Euconulus chersinus polygyratus</i>	0.230	0.011	-0.097
<i>Nesovitrea electrica</i>	0.244	0.136	-0.048
<i>Nesovitrea identata identata</i>	0.249	-0.033	-0.085
<i>Paravitrea significans</i>	0.082	-0.030	-0.321
<i>Hawaiiia minuscula minuscula</i>	0.179	-0.180	0.166
<i>Striatura milium</i>	0.091	0.385	0.351
<i>Striatura meridionalis</i>	0.091	0.386	0.350
<i>Zonitoides arboreus</i>	0.247	-0.108	-0.011
<i>Anguispira alternata alternata</i>	0.258	0.061	-0.130
<i>Heliocodiscus parallelus</i>	0.180	-0.236	0.149
<i>Punctum minutissimum</i>	0.167	0.238	0.053
<i>Philomycus carolinianus</i>	0.204	0.028	-0.266
<i>Succinea concordialis</i>	0.110	0.141	0.161
<i>Camilella vagans</i>	0.070	0.186	0.169
<i>Sirobilops labyrinthicus</i>	0.254	0.102	-0.195
<i>Gastrocopta armifera</i>	0.188	-0.254	0.199
<i>Gastrocopta contracta</i>	0.244	-0.113	-0.009
<i>Gastrocopta pentodon</i>	0.189	0.099	-0.174
<i>Gastrocopta tappaniana</i>	0.160	-0.089	0.066
<i>Gastrocopta procera procera</i>	0.151	-0.222	0.262
<i>Pupoides albilabris</i>	0.167	-0.230	0.199
<i>Vallonia parvula</i>	0.157	-0.282	0.286
<i>Carychium exile exile</i>	0.214	0.247	-0.013

Relationships between species distributions and climatic gradients

Table 2 gives the correlations between the first three principal components and the values for each of the seven climatic factors for each county. It is clear, for example, that the first component is strongly positively correlated with total precipitation ($r = 0.730$, $P < 0.001$) and with summer pre-

cipitation ($r = 0.721$, $P < 0.001$), but strongly negatively correlated with longitude ($r = 0.730$, $P < 0.001$). As might be expected from the mid-continental location of Kansas, there is a strong positive correlation between annual and summer precipitation ($r = 0.997$, $P < 0.001$). Furthermore, this state partly was chosen for this study because of the strong relationship ($r = 0.981$, $P < 0.001$) between longitude and precipitation, with a remarkably linear gradient from the wetter east to the drier west (see Figure 3). However, Figure 4 demonstrates that annual precipitation is a good predictor of the first principal component only for the eastern counties, where there generally is a higher diversity of gastropod species (Figure 5). A much better predictor of the first component ($r = 0.976$, $P < 0.001$) is simply the species diversity (Figure 6), although as noted above not all species load positively on this component. Furthermore, the superposition of many of the western counties along the first component that was evident before can be explained, in large part, by their depauperate gastropod populations.

The second principal component is most strongly positively correlated with latitude ($r = 0.303$, $P < 0.01$) and negatively correlated ($r = 0.203$, $P < 0.01$) with annual temperature (Table 2). Since higher latitudes generally correspond with lower temperatures over the counties of Kansas ($r = 0.800$, $P < 0.001$), these relationships imply that the second most important axis of gastropod species distribution can be explained partially by a second, less pronounced climatic gradient. The third principal component correlates only weakly with climatic variables; the highest correlation is with summer precipitation, but it is not statistically significant ($r = 0.150$, $P > 0.05$).

Principal components analysis of distributions of 28 selected gastropod species

In order to test the robustness of these results, a second principal component analysis was undertaken using a subset consisting of 28 of the 64 gastropod species found in Kansas. Table 1 indicates in boldface type the species selected for this analysis, which represent most of the families of gastropods. They include most of the species that loaded highly in the analysis of the full dataset, as listed above. Figure 7 shows the disposition of the 105 counties in the space defined by the first two principal components. Again, a longitudinal trend is evident (with most of the western counties superimposed), plus the separation of B4 (Anderson County) along the second component.

The first principal component in this case loaded positively on all 28 species (see Table 3), with the highest contributions provided by *Anguispira alternata*, *Strobilops labyrinthicus*, *Nesovitrea indentata*, *Zonitoides arboreus*, *Nesovitrea electrina*, *Gastrocopta contracta*, and *Euchemotrema leai*. Many of these same species contributed highly to the first component of the full 64-species dataset. Once again, scores on the first component across the counties of Kansas were highly positively correlated with the climatic factors of annual precipitation ($r =$

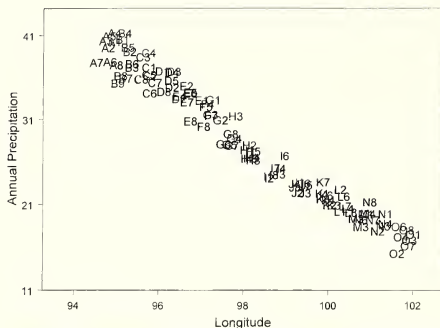


Figure 3. Relationship between longitude and total annual precipitation in Kansas.

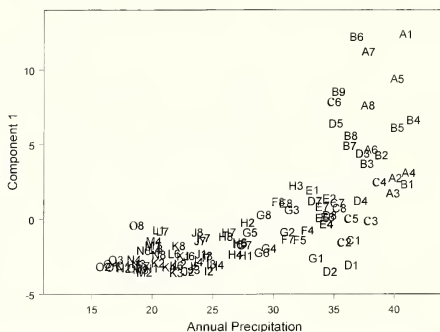


Figure 4. Relationship between total annual precipitation and scores on the first principal component of gastropod species distributions in Kansas.

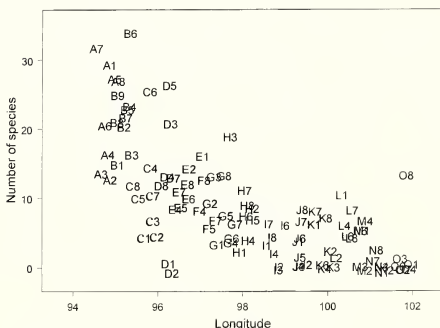


Figure 5. Relationship between longitude and gastropod species diversity in Kansas.

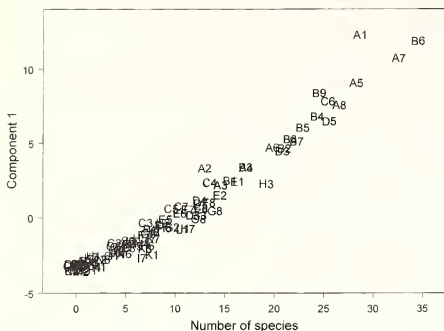


Figure 6. Relationship between gastropod species diversity and the first principal component.

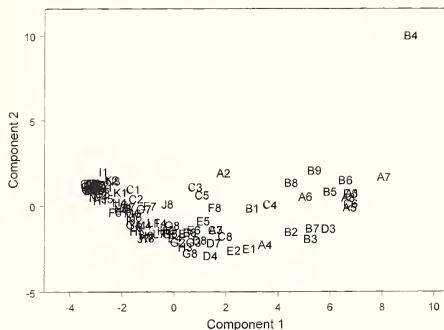


Figure 7. Location of the counties of Kansas in the space defined by the first two principal components based on the distribution of 28 gastropod species.

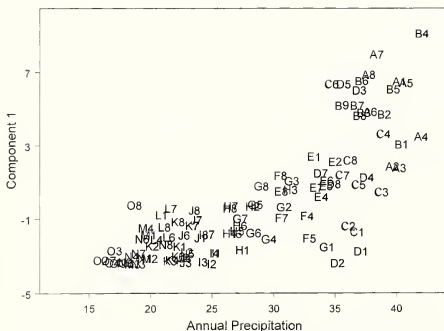


Figure 8. Relationship between total annual precipitation and scores on the first principal component of 28 gastropod species distributions in Kansas.

0.784, $P < 0.001$; Figure 8) and summer precipitation ($r = 0.781$, $P < 0.001$), were highly negatively correlated with longitude ($r = 0.773$, $P < 0.001$), and were very strongly correlated with species diversity ($r = 0.966$, $P < 0.001$).

The second principal component most strongly contrasted the distributions of *Striatura meridionalis*, *Striatura milium*, *Carychium exile*, and *Punctum minutissimum* with those of *Vallonia parvula*, *Gastrocopta armifera*, *Helicodiscus parallelus*, and *Pupoides albilabris*. This component was significantly correlated only with latitude ($r = 0.238$, $P < 0.05$). The third component contrasted the distributions of *Striatura meridionalis*, *Striatura milium*, *Vallonia parvula*, and *Gastrocopta procera* with those of *Mesodon thyroidis*, *Paravitrea significans*, and *Philomycus carolinianus*. It was correlated significantly only with two climatic variables: positively with latitude ($r = 0.372$, $P < 0.01$) and negatively with average temperature ($r = 0.231$, $P < 0.05$); of course, these two variables are correlated negatively with each other, as noted above.

The congruence of the results for the full set of 64 gastropod species found in Kansas and the selected subset of 28 species strengthens our interpretation that there has been a significant biotic response of this group of gastropods to climatic gradients in precipitation (from east to west across the checkerboard of Kansas counties) and, less strongly, in annual temperature (from south to north). These conclusions are comparable to the similarly strong response found by Kadmon and Heller (1998) of the land snails of Israel to a strong rainfall gradient from north to south. To our knowledge, the present study represents the first analysis of the relationship between land snail distributions and climatic factors in the central region of the United States.

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CHANGES IN THE FRESHWATER MUSSEL (MOLLUSCA: BIVALVIA) FAUNA OF THE CUYAHOGA RIVER, OHIO, SINCE LATE PREHISTORY

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ABSTRACT

We provide new information from archaeological samples on the historical freshwater mussel fauna (Mollusca: Bivalvia: Unionoidea) of the Cuyahoga River (South Park site: occupied between ca. A.D. 950 and 1650) and Black River (White Fort site, occupation centered at ca. A.D. 1350), northeast Ohio. Data from these prehistoric sites are compared with information on extant mussel populations of the Cuyahoga River published between 1890 and 2000. The high representation at both archaeological sites of the species *Actinonaias ligamentina*, *Elliptio dilatata*, and *Ptychobranchius fasciolaris* suggests that these were among the important clean water species in northeast Ohio prior to European settlement. By comparison, the modern mussel fauna of the lower Cuyahoga River (between Cleveland and Akron) contains none of these relatively abundant species, or any of the species represented in the archaeological material. The modern fauna of the lower river was established during the 20th century. This fauna is a low diversity assemblage of pollution tolerant species represented by rare live individuals. The modern mussel fauna of the upper Cuyahoga River (between Akron and the source) suggests that the upper and lower reaches are effectively isolated from each other. Published records indicate little change in the fauna during the last three quarters of the 20th century. Nevertheless, overall diversity, although substantially higher than that of the lower river, is considerably lower than that of the Grand River, which is located to the east of the Cuyahoga. Overall, the mussel fauna of the Cuyahoga River has changed greatly over time, most notably in terms of losses in diversity of clean water species and overall abundance.

Introduction

Freshwater mussels (Mollusca: Bivalvia: Unionoidea) are perhaps the most threatened group of animals in North America. Williams et al. (1993) reported that over 40 percent of the nearly 300 freshwater mussel taxa in the United States and Canada are considered extinct, endangered or threatened. Of the some 80 species that have occurred in Ohio, Watters (1996) reported that at least two-thirds are listed as extinct, extirpated, endangered, threatened, or of "special concern." This decline in species diversity followed at least 6000 years of stability preceding the diminution of eastern U.S. forests by European settlers (Bogan, 1990).

This study describes the changes that have taken place in the freshwater mussel composition (Family Unionidae) of the Cuyahoga River (Figure 1). The Cuyahoga River arises about 30 miles east of Cleveland, Ohio. It flows southwestward toward Akron and then describes a "U" as it turns to the northwest and empties into Lake Erie at Cleveland Harbor. The river is approximately 100 miles long. The section above Akron, which includes the source, is referred to as the "upper" part of the river. The section between Akron and the river's mouth is referred to as the "lower" Cuyahoga. The Cuyahoga River has been of critical importance to the history and economic development of Cleveland and northeast Ohio (Rose, 1950, p. 26, 69, 89, and 116, for example).

The extant freshwater mussels of the Cuyahoga River have been described scientifically beginning with Dean (1890). The most recent study has been by Smith (2000), who focused on mussel occurrence in the lower river within the Cuyahoga Valley National Park (formerly the Cuyahoga Valley National Recreation Area).

In this paper, we provide new information from archaeological specimens on the historical freshwater mussel fauna of the Cuyahoga River. Archaeological mussel data from the Black River, Lorain County, Ohio, are provided for comparison. Data from these prehistoric sites are then correlated with information from the literature on extant populations published between 1890 and 2000. Previous studies from other areas that have compared recent mussel distribution and ecology with archaeological data have been successful in reconstructing aquatic paleoenvironments and inferring environmental changes through time (e.g., Morey and Crothers, 1998; Hughes and Parmalee, 1999).

This study provides a view of the pre-European settlement mussel fauna of the relatively pristine Cuyahoga River. By comparing this fauna with the ones that followed, it is possible to see the multifarious effects of settlement and associated land use on an important component of the river's ecosystem. Also, knowing the fauna of the relatively pristine river provides information of potential use if the relatively stressed river of today is ever sufficiently restored to allow the re-introduction of the historical clean water species. Finally, bringing together the new and previously published data sets provides a longitudinal view of mussel



Figure 1. Cuyahoga River watershed and the location of the South Park collection site.

populations that is unique not only for the Cuyahoga River, but also for all of northeast Ohio.

Materials and Methods

Archaeological contexts of identified bivalve samples

All the bivalve specimens examined for this study were selected from archaeological samples recovered from the South Park site (33Cu8; 41°22'43.80" N, 81°37'20.97" W) and the White Fort site (33Ln3; 41°24'53.28" N, 82°6'30.42" W). The South Park site is located on an isolated upland ridge spur (elevation of 220 m a.s.l.) that extends northwestward into the valley of the lower Cuyahoga River in Independence, Ohio. The White Fort site is located on a flat, sandy bluff (elevation of 207 m a.s.l.) that overlooks the Black River Valley in northern Elyria Township, Lorain County, Ohio. Extensive archaeological excavations under the direction of David S. Brose (Case Western Reserve University and The Cleveland Museum of Natural History) were carried out at the South Park site between 1968 and 1981 (Brose, 1994). The White Fort site was investigated from 1995 to 1998 by one of us (Redmond, 1999). Both sites are believed to represent semi-permanent, maize-agricultural village settlements. The major archaeological components at both the South Park and White Fort sites fall within the Late Prehistoric period, but South Park is affiliated with the Whitlesey cultural tradition (Brose 1994, p. 30–31), and White Fort with the Sandusky tradition

Table 1. Associated radiocarbon determinations of archeological specimens.

Lab. no.	Conventional age	Calendrical date	Calibrated intercepts	Calibrations (Vogel et al., 1993)	
				1 sigma	2 sigma
SOUTH PARK					
WIS 537 (Fea. 1)	310 ± 50 BP	A.D. 1640	A.D. 1638	A.D. 1495 to 1653	A.D. 1449 to 1952
CWRU 4 (Fea. 4)	305 ± 55 BP	A.D. 1645	A.D. 1640	A.D. 1495 to 1656	A.D. 1447 to 1953
WIS 538 (Fea. 49)	380 ± 55 BP	A.D. 1570	A.D. 1489	A.D. 1443 to 1633	A.D. 1429 to 1650
WHITE FORT					
Beta 90565 (Fea. 95-10)	670 ± 50 BP	A.D. 1280	A.D. 1300	A.D. 1285 to 1315& A.D. 1345 to 1390	A.D. 1270 to 1405
Beta 110713 (Fea. 95-10)	600 ± 50 BP	A.D. 1350	A.D. 1395	A.D. 1305 to 1410	A.D. 1290 to 1425
Beta 110714 (Fea. 95-10)	600 ± 40 BP	A.D. 1350	A.D. 1395	A.D. 1310 to 1365& A.D. 1375 to 1410	A.D. 1295 to 1420
Beta 90566 (Fea. 95-16)	370 ± 50 BP	A.D. 1580	A.D. 1495	A.D. 1455 to 1535 & A.D. 1545 to 1635	A.D. 1435 to 1650

(Stothers et al., 1994). According to Brose (1994), the South Park site provides evidence for as many as three temporally sequential village occupations that occurred between approximately A.D. 950 and 1650. Bivalve specimens were recovered from each of these cultural levels. In contrast, temporally sensitive archaeological remains from the White Fort site indicate a single major village occupation centered at ca. AD 1350 (Redmond, 1999, p. 141).

The bivalve specimens identified in this study were recovered from archaeological deposits that consisted of food residues and broken tools, ornaments, and other implements that were discarded by the village inhabitants. At both the South Park and White Fort sites such material was most often deposited into empty pits previously used for food storage or cooking. In a few cases, shell and other debris were discarded onto surface dumps (midden features) or into shallow trenches that originally served as foundations for the walls of oval- to circular-shaped dwellings. Regardless of context, all but one of the identified bivalve specimens are culturally unmodified and thus most likely represent the remains of freshwater mussels that were gathered and consumed by the inhabitants of each village site. One specimen from the South Park site, identified as *Actinonaias ligamentina carinata* (CMNH Archaeology Collection 5948), exhibits a one centimeter-wide perforation which indicates that the shell was originally modified to tie a handle so that the shell could be used as a spoon, hoe, or other kind of implement.

Identified bivalve specimens were recovered from radiocarbon dated contexts at both the South Park and White Fort sites (Table 1). In the South Park site sample, shell fragments from Features 1 and 4 (pit features) were associated with

wood charcoal that produced uncalibrated radiocarbon dates of A.D. 1640 \pm 50 and A.D. 1645 \pm 55 respectively (Brose, 1994, p. 171; 168). Charcoal from Feature 49 (pit feature) resulted in an uncalibrated date of A.D. 1570 \pm 55 (Brose, 1994, p. 171). Bivalve samples from the White Fort site were recovered from two dated contexts. Feature 95-10 (a structural trench) contained abundant shells in association with charcoal samples that produced uncalibrated dates of A.D. 1280 \pm 50, A.D. 1350 \pm 40, and A.D. 1350 \pm 50 (Redmond, 1999, p. 141). Charcoal from Feature 95-16 (pit feature) resulted in an uncalibrated date of A.D. 1580 \pm 50 (Redmond, 1999, p. 141).

Both the uncalibrated and calibrated radiocarbon results derived from the South Park features and Feature 95-10 at White Fort support the proposed temporal spans for each site's occupation. The uncalibrated late sixteenth century date from White Fort Feature 95-16 appears to be too recent in age when compared to associated ceramic temporal indicators; however, it may date an as-yet unrecognized Late Prehistoric period occupation of the village site (Redmond, 1999).

Sample selection

All bivalve specimens observed in the South Park site and White Fort site collections represented either single valves or fragments of single valves. No articulated specimens were discovered, and all specimens were devoid of periostracum. Mussel shells were chosen for study based on their preservational state. Generally, at least 40 percent of the valve needed to be present to provide enough material for identification to the species level. All of the mussels from both collections belonged to the family Unionidae and were identified by reference to Watters (1995).

Results and Discussion

Table 2 summarizes the results of this study. The new data on archaeological specimens from the White Fort site and South Park site are summarized to the left in the table. Results of surveys of extant mussels are summarized to the right of these in chronological order, beginning with the findings of Dean (1890) and then Ortmann (1924). The "upper Cuyahoga" occurrences combine the results of Huehner (1985), Hoggarth (1990), and Huehner and Gyulai (1999). The "lower Cuyahoga" occurrences are from Smith (2000) and Smith et al. (2002); Tinkers Creek occurrences are from Krebs et al. (2002).

Together, these data show that the distribution, abundance and species composition of mussels in the Cuyahoga River have changed extensively since European colonization of the watershed. The seven sets of survey data in Table 2 highlight the substantial loss of species in the lower portion of the Cuyahoga, while the upper, less industrially impacted reaches of the river have changed little in the last 100 years.

Based on archaeological data from the South Park site, a diverse mussel community existed that may have been dominated by five species: *A. ligamentina carinata*, *Ambleria plicata*, *Elliptio dilatata*, *Ligumia recta*, and *Psychobranchus fasciolaris*. All of these latter species produce large, robust shells that should preserve well, and Watters (1995) describes each as generally abundant within the habitats where they are found. Eight additional species were less frequently encountered in the collections. All of these species are either rare in Ohio today, or possess small or fragile shells (Morey and Crothers, 1998). Two of these 13 species (*A. plicata* and *P. fasciolaris*) had apparently disappeared by the late 1800s, when Dean (1890) surveyed the river, although eroded shells of the former species still occur in the river today. Likewise, Morey and Crothers (1998) describe shells of four additional species not found in the archaeological material but present in the modern surveys (*Lampsilis fasciola*, *Lasmigona costata*, *Potamilius alatus*, and *Strophitus undulatus*) as sufficiently fragile to make under-representation in collections of ancient material a likely possibility. Nevertheless, an historical abundance likely explains why old, eroded shells of four of the five more commonly found species are still found as eroded shells in the Cuyahoga River (Smith, 2000; Smith et al., 2002).

The overall taxonomic similarity of the South Park and White Fort samples suggest that these collections provide important clues to the list of mussel species characteristic of northeastern Ohio rivers at a time prior to European settlement. The high representation at both archaeological sites of the species *A. ligamentina carinata*, *E. dilatata*, and *P. fasciolaris* suggests that these were among the more important clean water species, both ecologically and as a food resource, during late prehistory.

The modern composition of the lower Cuyahoga has changed greatly over time, and may contain as few as six species. In addition, because extensive survey work turned up

only four live specimens and few fresh shells, it is also safe to conclude that mussels are rare in the lower Cuyahoga today. The live specimens which have been found are of the following three species: *Potamilius alatus*, *Pyganodon grandis*, and *Quadrula quadrula* (Smith, 2000; Smith et al., 2002). Of these, only *Potamilius alatus* was found by Dean (1890). *Pyganodon grandis* was previously reported only from the upper Cuyahoga (Ortmann, 1924) and *Q. quadrula* had not been reported before the work of Smith (2000) and Smith et al. (2002), although both species existed in Lake Erie prior to the introduction of zebra mussels (Ortmann, 1919).

Other species that may exist in the lower Cuyahoga include *Fusconaia flava*, *Lasmigona compressa*, and *Leptodea fragilis*, for which fresh shells were found (Smith, 2000; Smith et al., 2002). As is the case for *Q. quadrula*, the latter of these three species was also a new record for the Cuyahoga. *Fusconaia flava* was a common species in the last century and it is one of the few small species represented in the archaeological data, which may be biased towards larger species because the mussels were collected for food. Although *F. flava* has never become established in the upper Cuyahoga, this species is common today in Tinkers Creek, which may have provided a refuge when the river became polluted. Alternatively, Metcalf-Smith et al. (2000) describe *F. flava*, *P. grandis*, *P. alatus*, and *Q. quadrula* as possibly the most pollution tolerant of species living in the Grand River (Southwestern Ontario).

In contrast to the lower Cuyahoga, the unionid fauna of the upper part of the Cuyahoga River has changed little. Ortmann (1924) reported finding *Anodontoidea ferussacianus*, *Lampsilis radiata luteola*, *Lasmigona costata*, *Lasmigona compressa*, *Ligumia nasuta*, *P. grandis* (not found by Dean, 1890), *S. undulatus*, and *Utterbackia imbecillis*. All of these species remain in the upper river (Huehner, 1985; Hoggarth, 1990; Huehner and Gyulai, 1999), and added to them is the now common *Lasmigona complanata*, which Dean (1890) found in the local canals. The stability of this community suggests effective isolation of the upper from the lower river. These eight species suggest good diversity, but the Grand River (Lake Co., Ohio), long considered one of the cleanest of the rivers in northeast Ohio, contained 17 species in the early 1900s (Ortmann, 1924).

This geographical isolation of populations also applies to the mussel communities of Tinkers Creek, a smaller stream, which, while not as heavily influenced by industry, slowly winds through agricultural and more suburban communities as it passes through the Twinsburg and Brecksville areas. Five species are common in Tinkers Creek (Table 2) and fresh shells of three others occur occasionally. The greatest contrast between the Cuyahoga River and Tinkers Creek is the presence of *F. flava* and possibly *Alasmidonta marginata* (three fresh shells) in Tinkers Creek. The biota of this tributary is clearly related to the lower Cuyahoga of the late 1800s and not to the fauna of the relatively pristine upper river.

Table 2. Historical distribution and abundance of unionid mussels in the Cuyahoga River watershed. Most species names are used in the sense of Watters (1995). Shell size indicates the largest expected size for Ohio forms (Watters, 1995). Old specimens are those showing extensive wear to the shells and complete loss of the periostracum. Data for the extant populations derive from Huehner (1985), Hoggarth (1990), Huehner and Gyulai (1999), Smith (2000), and Krebs et al. (2002).

Species	Shell size max. diam. (cm)	Black R. (White Fort) prehistoric shells	Cuyahoga R. (South Park) prehistoric shells	Cuyahoga (Dean, 1890)	Upper Cuyahoga (Ortmann, 1924)	Upper Cuyahoga shells	Upper Cuyahoga live mus- sels	Lower Cuyahoga shells	Lower Cuyahoga live mussels	Tinkers Creek shells	Tinkers Creek live mussels
<i>Actinonaias ligamentina carinata</i>	15	7	40	present				29 old		2 old	
<i>Alasmodonta marginata</i>	10			present						3	
<i>Amblema plicata</i>	15	1	45					11 old			
<i>Anodontoides ferrussacianus</i>	10			present	present	2	11				
<i>Cyclonaias tuberculata</i> *	12		1								
<i>Elliptio dilatata</i>	12	13	50	present				3 old			
<i>Fusconaia flava</i>	10		2	common				7		16	12
<i>Lampsilis cardium</i>	15	20	2	present				1 old			
<i>Lampsilis fasciola</i> [†]	10			present							
<i>Lampsilis radiata luteola</i>	12	1	2	present	present	116	334			31	1
<i>Lasmigona complanata</i>	15			canal		110	274				
<i>Lasmigona compressa</i>	10			present	present	15	33	1		11	11
<i>Lasmigona costata</i> [†]	12	1		present	present	26	63	3 old		13	17
<i>Leptodea fragilis</i>	15							3			
<i>Ligumia nasuta</i> **	10			present	present	51	87				
<i>Ligumia recta</i> *	25	2	15	present							
<i>Obovaria subrotunda</i>	7	3	5	present							
<i>Pleuroberma sintoxia</i> *	12		6	present				1 old			
<i>Potamilus alatus</i> [†]	20			present				1	2		
<i>Ptychobranchius fasciolaris</i>	15	48	23								
<i>Pygodon grandis</i>	15				present	530	1171	3		153	77
<i>Quadrula quadrula</i>	10									1	
<i>Strophitus undulatus</i> [†]	10			present	present	14	38				5
<i>Toxolasma parvus</i>	4	1		reservoirs							2
<i>Utterbackia imbecillis</i>	10				present	3	9				
<i>Villosa iris</i>	7			present							
Total specimens		97	191	NA	NA	867	2020	15	4	234	118

[†] Identifies fragile shells, which may therefore be underrepresented in the midden analysis (Morey and Crothers, 1998).

* Special concern and threatened species

** Ohio endangered species

Conclusions

The similarities between the species lists compiled for the White Fort and South Park sites provide clues to the mussel fauna that inhabited the relatively pristine rivers of northeast Ohio prior to European settlement. The high representation at both archaeological sites of the species *A. ligamentina carinata*, *E. dilatata*, and *P. fasciolaris*, in addition to the large number of *A. plicata* at the South Park site, suggests that these were among the important clean water species in northeast Ohio prior to European settlement. The presence of their shells today verifies past abundance of at least three of the four species. Live specimens of *A. ligamentina carinata* and *E. dilatata* have not been reported since collections by

Dean (1890), while by contrast, *A. plicata* and *P. fasciolaris* must have disappeared prior to the industrialization of the Cuyahoga River valley. Therefore, *A. ligamentina carinata* and *E. dilatata* are particularly good candidates for reintroduction into northeast Ohio streams once these streams have been restored to a cleaner condition. The modern fauna of the lower river was established during the 20th century and may be characterized as a relatively low diversity assemblage of pollution tolerant species represented by a low number of individuals. The modern Tinkers Creek fauna, by comparison, is possibly a "refugium fauna" of species characteristic of the lower Cuyahoga in the late 19th century.

The modern mussel fauna of the upper Cuyahoga clearly

tells a tale of two rivers, where the upper and lower reaches are effectively isolated from each other. Published records indicate little change in the fauna during the last three quarters of the 20th century. Nevertheless, overall diversity, although substantially higher than that of the lower river, is considerably lower than that of the Grand River (Lake Co., Ohio). Moreover, it does not resemble the fauna reflected in the archaeological samples.

Overall, the mussel fauna of the Cuyahoga River has changed greatly since late prehistory, most notably in terms of losses in diversity of clean water species and overall abundance.

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A STUDY OF THE UNIONIDAE OF TINKERS CREEK, OHIO

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ABSTRACT

We present data on freshwater mussel (Mollusca: Bivalvia: Unionidae) distributions for Tinkers Creek, a small Ohio stream that previously had not been surveyed for its unionid fauna. The distribution of these mussels was mapped against the changing habitat of the stream, with special attention paid to two zones of human manipulation, a wastewater treatment plant and a stretch of the river where the bed was relocated to enable development. At least five unionid species live in Tinkers Creek. These are *Pyganodon grandis*, *Lampsilis radiata luteola*, *Fusconaia flava*, *Lasmigona costata*, and *Lasmigona compressa*. Fresh shells suggested the presence of three others: *Strophitus undulatus*, *Toxolasma parvus*, and *Alasmidonta marginata*. The region of Tinkers Creek where the mussels are most common extends through Twinsburg, Ohio, and upstream to a waterfall just below the confluence with Pond Brook. Relocation of the river channel eliminated mussels from a 0.5 km stretch in eastern Twinsburg. Furthermore, the impact of effluent from a wastewater treatment plant was minor, at most. Mussel diversity diminished from five to three species commonly found below this facility. A change in river habitat to faster flow, however, provided an alternate explanation for this faunal change. The most striking difference was the replacement of *Lasmigona costata*, a species usually found in medium and large rivers, by *L. compressa*, a species common in small streams and headwaters.

Introduction

Freshwater mussels (Mollusca: Bivalvia), particularly the family Unionidae, are in steady decline in diversity worldwide, but they remain an important component of freshwater ecosystems. Freshwater mussels live infamously to semi-faunally in bottom sediments and sustain themselves by suspension feeding. Their methods of feeding and burrowing serve not only to remove seston from the water column and to transfer it to the sediment-water interface, but also to mix and to irrigate bottom sediments significantly. These activities have a major impact on nutrient cycling in the environment (McCall et al., 1986).

Because freshwater mussels routinely take in water while feeding and are sensitive to pollutants during different stages of their complex life cycle, unionids are good indicators of water quality (Ortman, 1909, p. 94). Common contaminants that affect mussels include heavy metals, pesticides and herbicides, nitrogen, phosphorus, and trace metals (Havlik and Marking, 1987). Eastern North America has been home to the richest freshwater mussel fauna in the world (Cummings and Mayer, 1992, p. 1), but like the abundance of many aquatic organisms, unionid numbers have declined due to habitat alteration, pollution, isolation and impoundments,

sedimentation, and competition from nonnative species (National Native Mussel Conservation Committee, 1998).

As a consequence of environmental degradation, mussels receive statewide protection in Ohio. This protection, however, is not fully effective unless faunal studies are kept up-to-date. In addition, no data exist for many streams. A diverse mussel population in a lake or stream may be an indication of good water quality; contrastingly, the absence or decline of mussels above or below regions where diverse populations exist may be an indicator of habitat degradation. As a result, a mussel survey may be a very cost-effective way to initially identify a potential pollution problem, or to clear a suspected source from suspicion of environmental impact.

We investigated species composition of freshwater mussels in Tinkers Creek, a fifth order stream located in northeast Ohio (Figure 1). Tinkers Creek became an area of interest for several reasons. First, no comprehensive data set has yet been assembled on the number and species of mussels inhabiting this important tributary of the Cuyahoga River. For example, a previous study (Smith, 2000; Smith et al., 2002) found no mussels in the lower region of Tinkers Creek within the Cuyahoga Valley National Park. Second, a number of wastewater treatment plants (WWTP) occur along the stream, and one outflow occurs in the middle of the city of Twinsburg, Ohio, an area largely passed over in a recent EPA analysis (Ohio EPA, 1994). Nevertheless, the section of the stream in and near Twinsburg remains one of the best maintained regions of the stream for recreational use. We compared species composition upstream and downstream of this recreational area. Lastly, a 500 m section of the streambed was relocated to facilitate development in eastern Twinsburg (Army Corp of Engineers permit 9451210), and we were interested to see if this change affected mussel diversity.

Materials and Methods

A field study was conducted from May through July of 2000. Field collection was performed visually (sites 15–17), as well as by brailing with feet or hands (all other sites) where either turbidity or depth prevented a visual search of the stream bottom. Search sites were concentrated near (but not restricted to) areas below riffles, where the water is most highly oxygenated, enhancing living conditions for mussels. We also assessed dissolved oxygen levels, pH, conductivity, water temperature and substratum composition.

The search method was determined at each site. In areas where water was above 1 m (high water), searching was restricted to feeling along the bottom with soft rubber shoes; at less than 1 m, we also felt along the bottom with our hands, while in very shallow water, mussels could be visually identified. Visibility was usually at best about 15 cm. The total survey time spent at each location surveyed by brailing averaged 35 minutes (range 30–40 minutes). When live specimens were found, they were arranged on the bank by species, identified preliminarily and counted, and photographs were taken to con-

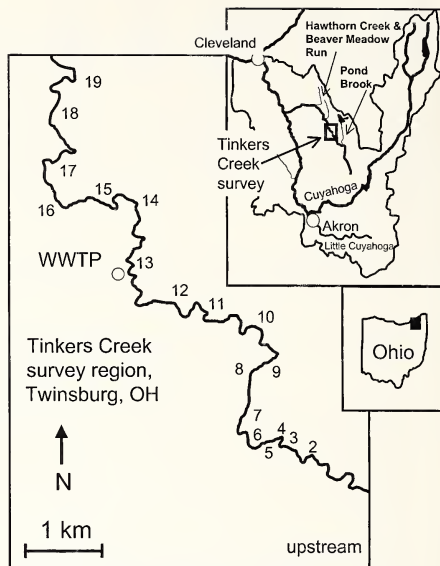


Figure 1. Map showing sampling sites 2–19 along 10 km of Tinkers Creek. This stream is the largest tributary of the Cuyahoga River (inset). The stretch of the Tinkers Creek shown flows through the city of Twinsburg, Ohio, which lies between the confluence of Tinkers Creek and Pond Brook Run upstream, and the confluence with Beaver Meadow Run downstream. Site 1 is located off the map to the east.

firm identifications. Mussels then were gently placed back where they had been found. Empty shells were collected, numbered (37–131; 174–236; 244–349), and identified. These are presently stored in the Department of Biological, Geological, and Environmental Sciences at Cleveland State University.

Results and Discussion

A total of 138 living mussels of five different species were found in Tinkers Creek (Table 1). *Pyganodon grandis* (Say, 1817) comprised 65 percent of the living specimens found, *Fusconaia flava* (Rafinesque, 1820) 15 percent, *Lasmigona costata* (Rafinesque, 1820) 11 percent, *Lasmigona compressa* (Lea, 1829) eight percent, and *Lampsilis radiata luteola* (Lamarck, 1819) one percent (a single female specimen, although shells of this species were common). The apparent rarity of live specimens of this latter species may perhaps be explained by its life position, which is approximately 2/3 buried (Tevesz et al., 1985, p. 31), while the other species often were

Table 1. The distribution and abundance of unionid mussels in Tinkers Creek based on collections of both shells and live mussels. The frequency of each species in the collections is indicated in parentheses to the right of the total number of individuals.

Species in Tinkers Creek	Above outflow Live mussels	Above outflow Shells	Below outflow Live mussels	Below outflow Shells	Tinkers Creek ¹ Live mussels	Tinkers Creek ¹ Shells
<i>Alasmodonta marginata</i>		1 (0.01)		2 (0.02)		4 (0.01)
<i>Fusconia flava</i>	18 (0.19)	13 (0.07)	1 (0.03)	3 (0.03)	21 (0.15)	23 (0.06)
<i>Lampsilis radiata luteola</i>	1 (0.01)	18 (0.10)		12 (0.10)	1 (0.01)	35 (0.09)
<i>Lasmigona compressa</i>	5 (0.05)	2 (0.01)	5 (0.16)	8 (0.07)	11 (0.08)	11 (0.03)
<i>Lasmigona costata</i>	15 (0.16)	6 (0.03)		8 (0.07)	15 (0.11)	18 (0.05)
<i>Pygodon grandis</i>	57 (0.59)	141 (0.76)	26 (0.81)	76 (0.66)	90 (0.65)	280 (0.73)
<i>Strophitus undulatus</i>		2 (0.01)		5 (0.04)		9 (0.02)
<i>Toxolasma parvus</i>		3 (0.02)		1 (0.01)		4 (0.01)
Total specimens	96	186	32	115	138	384

¹Totals for Tinkers Creek include data from a preliminary survey (1999) that did not distinguish locality with respect to the WWTP. The data presented here also include additional material to that summarized in Tevesz et al. (2002).

well exposed on firm substrate. Alternatively, this species, which Watters (1995, p. 59) describes as the most widespread and common in Ohio, may be in decline within this stream. *L. costata* and *F. flava* frequently were found in close proximity to each other, and *P. grandis* co-occurred with all other species.

The primary area inhabited by mussels is restricted to a region of the stream within Twinsburg, Ohio, and the upstream limit is just below the confluence of Tinkers Creek with Pond Brook (Figure 1). At Pond Brook, the stream appears more as a riverine wetland; it slows and the Ohio EPA (1994, p. 18) reports a minimum dissolved oxygen (DO) concentration of 3.0 mg/l just upstream of Pond Brook, which may approach the threshold for survival of some mussel species (Vaughn and Taylor, 1999; Chen et al., 2001). No living mussels or even shells were found in this region, nor in surveys of the stream within Tinkers Creek State Park, east of Twinsburg and further upstream of Pond Brook. About 500 meters below the confluence with Pond Brook, Tinkers Creek broadens, runs across a lengthy riffle bed, and drops about a meter over a small natural waterfall. Below this fall, DO approached saturation, and a 2 h survey produced one live *L. costata* (site 1, Table 2) and a half valve from *L. r. luteola*. Thus, this region may be the upper limit for the distribution of unionids in Tinkers Creek. The downstream limit is at least 3 km above the confluence of Tinkers Creek with the Cuyahoga River. Neither we nor Smith (2000) found live mussels, possibly because water conditions degrade rapidly below Twinsburg where Beaver Meadow Run brings effluent from the Solon wastewater treatment plant, as does Hawthorn Creek from Bedford Heights (Ohio EPA, 1994, p. 144–147). However, surveys in this industrial region have yet to be performed.

Across the survey area, changes in the presence, absence and distribution of mussels indicate their usefulness as a water quality indicator. The distribution of mussels along rivers often can be nearly continuous where impoundment does not degrade conditions, and the communities of mussels

present may correlate with the habitat (Morey and Crothers, 1998; Hughes and Parmalee, 1999). Our assessment of a 10 km stretch of Tinkers Creek was facilitated by its shallow (1 m) depth (Table 2), which enabled replicate sampling across short distances. Some mussels were found in almost every search, and where the water was sufficiently clear and shallow to see the stream bed of Tinkers Creek, mussels appeared to be distributed uniformly and crawling semi-infaunally (see also McCall et al., 1986, p. 96). Dissolved oxygen levels approached saturation throughout the summer, probably due to a high frequency of riffle beds.

The occasional absence of freshwater mussels within our survey of Tinkers Creek was restricted to areas of high levels of detritus on the stream bottom, or regions of bare rock (Table 2). Soft, muddy substrata also yielded few or no mussels (two sites, with one mussel). That 114 of 128 mussels inhabited firmer substrates of mixed sand, gravel and small rocks, but only 13 inhabited rocky areas support the importance of substrate to levels of abundance (Metcalf-Smith et al., 2000). The changes in the nature of the substrate also may slow the reestablishment of mussels in the newly created stream bed, which was rerouted in eastern Twinsburg by simply digging a two-meter deep trench. After two years, the substrate has firmed sufficiently for wading, but no mussels were found despite a diverse fauna both above and below this section (Table 2).

Mussels also thrived both above and below the WWTP located between sites 12 and 13 (Figure 2), although the relative abundance of some species shifted at or above this point in the stream (Figure 3). The Shannon-Weaver Index for mussels declined from only 1.07 above this site to 0.58 below the plant; both values suggest low diversity. Most of the mussels downstream were *P. grandis* followed in frequency by *L. compressa*. Only one other live specimen, a *F. flava*, was found downstream. Neither the significant decline in *L. costata* ($X^2 = 5.28$, $P < 0.05$) nor the comparative

Table 2. Site locations, habitat, species present and the number of unionid individuals found alive along a 10 km stretch of Tinkers Creek.

Location	Site no. (Fig. 1)	Latitude/Longitude	Bottom type	Living mussels found	Species present
Tinkers State Park, above Pond Brook		41°17.08' 81°23.58'	heavy detritus, soft mud	0	
Tinkers State Park, above Pond Brook			sand/rock/gravel	0	
Old Mill Rd., below falls	1	41°17.12' 81°24.37'	very rocky (small rocks)	1	<i>L. costata</i>
Above the altered site	2	41°18.40' 81°25.91'	sand/gravel	11	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i>
Above the altered site	3	41°18.45' 81°26.00'	sand/silt/gravel	4	<i>Fusconaia flava</i> <i>P. grandis</i>
Just above the altered site	4	41°18.48' 81°26.06'	sand/silt	2	<i>P. grandis</i>
Altered river site		41°18.48' 81°26.06'	sand/gravel	0	
Altered river site		41°18.51' 81°26.22'	rock/sand	0	
Just below the altered river site	5	41°18.51' 81°26.22'	mixed gravel/silt	8	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i>
Below the altered river site	6	41°18.56' 81°26.25'	sand/gravel	11	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i>
Just upstream of the Ravenna Rd. bridge	7	41°18.60' 81°26.48'	firm gravel/sand	13	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i>
Begin recreational zone Cannon Park	8	41°18.86' 81°26.23'	rock/gravel, shallow water - 18"	12	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i>
Cannon Park recreational zone	9	41°18.88' 81°26.19'	rocky	12	<i>Fusconaia flava</i> <i>L. costata</i> <i>P. grandis</i> <i>Lampsilis radiata luteola</i>
Recreational zone	10	41°18.88' 81°26.10'	sandy	8	<i>Fusconaia flava</i> <i>L. costata</i> <i>L. compressa</i> <i>P. grandis</i>
Recreational zone			soft mud, abundant detritus	0	
Just below Darrow Rd. bridge (State Rt. 91)	11	41°19.17' 81°26.50'	mixed/soft, some detritus	3	<i>Fusconaia flava</i> <i>P. grandis</i>
Recreational zone	12	41°19.20' 81°26.67'	sand/gravel	11	<i>L. costata</i> <i>L. compressa</i> <i>P. grandis</i>
Just downstream of outflow	13	41°19.45' 81°26.93'	soft and firm sand	7	<i>L. compressa</i> <i>P. grandis</i>
Specimen found on bank. None nearby			rock, muddy, no loose sand	1	<i>P. grandis</i>
Recreational zone	14	41°19.70' 81°26.90'	sand/gravel	6	<i>P. grandis</i>
Recreational zone			rocky	0	
Recreational zone	15	41°19.73' 81°27.09'	sand/gravel	8	<i>Fusconaia flava</i> <i>L. compressa</i> <i>P. grandis</i>

Table 2. Continued.

Location	Site no. (Fig. 1)	Latitude/Longitude	Bottom type	Living mussels found	Species present
Recreational zone	16	41°19.73' 81°27.30'	rock/sand, very shallow water	2	<i>P. grandis</i>
Center Valley Park, south end	17	41°19.96' 81°27.39'	sand/gravel	1	<i>P. grandis</i>
Recreational zone	18	41°20.28' 81°27.36'	rock/sand	5	<i>P. grandis</i>
Recreational zone	19		rock/gravel	0	
North end of Center Valley Park		41°20.37' 81°27.29'	sand/gravel	2	<i>P. grandis</i>
Bedford Reservation, east of 271		41°23.02' 81°30.37'	rock/gravel	0	0
Brecksville, west of 271		41°23.16' 81°32.27'	rocky	0	0
Confluence with the Cuyahoga		41°21.51' 81°36.35'	rock/gravel	0	0

decline in *F. flava* ($X^2 = 3.76$, $P < 0.10$), however, are sufficient to implicate the WWTP as a detriment to the stream.

Instead, change in the diversity of species may follow clearly visible shifts in the natural characteristics of Tinkers Creek. Just above the WWTP, near sites 10 and 11 along the survey (Figure 1), the stream changes depth and flow. Upstream of the plant depth is greater (1–2 m deep) and flow slower than downstream, where depth is less than one meter and the flow faster as the stream descends the escarpment east and south-east of Cleveland. *Lasimigona costata* prefers medium and large rivers, while *L. compressa* is a small stream species, but both require clean water (Watters, 1995, p. 62–63). Possibly as a consequence of structural change, the comparative frequency of *L. compressa* increased ($X^2 = 3.42$, $P < 0.10$).

In contrast to variation in live individuals, the relative frequency of shells of the different species provided no hint of change in conditions upstream or downstream of the WWTP. Of a total of 384 shells collected in the search region (Table 1), *P. grandis* was the most common, followed by *L. r. luteola*, *F. flava*, *L. costata*, and *L. compressa*. A few complete shells or valves were found for each of the following: *Strophitus undulatus* (Say, 1817), *Toxolasma parvus* (Barnes, 1823) and *Alasmidonta marginata* (Say, 1818). A single worn valve of *Actinonaias ligamentina* (Barnes, 1823) was found, but this species has probably disappeared from the entire watershed since its observance by Dean (1890) in the lower Cuyahoga. Therefore, while the river and its molluscan fauna have changed as the area developed (Tevesz et al., 2002), the only change in rank order of abundance when we considered extant species was the collection of fewer *F. flava* shells below the WWTP, a difference that was not significant. Thus the fauna may, at present, have stabilized.

Therefore, our use of mussels to identify changing condi-

tions along Tinkers Creek fairly supports the presence of the Twinsburg, Ohio, WWTP as a small factor or nonfactor to Tinkers Creek. Substrate and stream dynamics probably affect mussel populations more (Miller and Payne, 1998; Hardison and Layzer, 2001), as suggested by the shift to a shallower and faster current just above the plant that can explain why *L. costata* and *F. flava* make up a greater proportion of the fauna upstream rather than downstream, and why *L. compressa* increased in frequency downstream. That the shift is between these two *Lasimigona* species is very important, because each of the other three species found alive, particularly *P. grandis* and *F. flava* (Metcalf-Smith et al., 2000), are more tolerant of impoundment and moderate pollution.

Chemical analysis similarly supported this conclusion, as we found that water samples from the immediate area of the stream into which the WWTP drained differed only marginally from those downstream for dissolved oxygen and for pH. For example, the effluent region was more basic (pH 7.93), but the dissolved oxygen concentration (10.15 ppm) was higher than the average for all downstream sites (7.24 ppm). Also, EPA data show no exceedences of coliform bacteria, and the quantity of many chemical pollutants entering the Cuyahoga from Tinkers Creek has declined between 1984 and 1996 (Ohio EPA, 1994; 1999). Finally, the Invertebrate Community Index for this region of the stream met or exceeded requirements for recreational use after 1991, and stream quality remains good above the confluence with Beaver Meadow Run and Hawthorn Creek to the north (Ohio EPA, 1994).

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Figure 2. View of the Twinsburg wastewater treatment plant from the river (A) showing effluent and (B) a visual image of the proportional contribution that can be obtained from treatment plants when river water levels are low (photo taken looking upstream). Photos taken July 26, 2000.

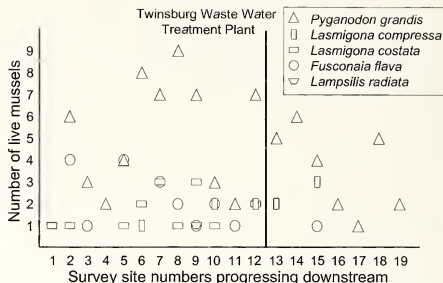


Figure 3. Diversity of mussels and number of each species collected in the survey of Tinkers Creek progressing downstream through a recreation preserve, past the Twinsburg wastewater treatment plant, and down to Center Valley Park in north Twinsburg.

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KIRTLANDIA[®]

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LIST OF FRESHWATER MUSSELS (UNIONOIDA) AT THE CLEVELAND MUSEUM OF NATURAL HISTORY

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ABSTRACT

Cataloged freshwater mussel (Bivalvia: Unionoida) specimens housed at The Cleveland Museum of Natural History are listed. The catalog number for each species, the number of lots and specimens, years and states of collection, and federal and Ohio state endangered status are given. The collection contains 5123 specimens in 1452 lots, representing 110 species from five families. Approximately one-third of all species in the collection are endangered, extirpated, or otherwise threatened according to Ohio or federal standards.

Introduction

Water quality deterioration has stressed numerous populations of aquatic organisms, including freshwater mussels (Bivalvia: Unionoida) (Strayer, 1999a). North America has the highest number of species of unionids in the world (Cummings and Mayer, 1992; Bogan, 1993; Parmalee and

Bogan, 1998; Nedeau et al., 2000) with some 300 species (Nedeau et al., 2000). Of the mussels endemic to North America, 75 percent are endangered, threatened, or species of special concern (Williams et al., 1993) with only 70 species stable throughout their range (Nedeau et al., 2000). The greatest declines have been found within the southeast-

ern United States where the highest numbers of species are located (Bogan, 1993). Insects and fishes are particularly well known as indicator organisms for determining habitat quality (Karr et al., 1986; Rosenberg and Resh, 1993). However, the use of freshwater mussels as indicators of water quality has been understudied (Strayer, 1999).

The declines have been caused by alteration of the habitats that the mussels are found in (Bogan, 1993). Impoundments, commercial exploitation, pollution, siltation, and habitat loss are contributing factors (Bogan, 1993; Brim-Box and Mossa, 1999; Waller et al., 1999). The introductions of the zebra and quagga mussels in the late 1980s have stressed endemic unionids even further (Schlosser and Napela, 1994; Ricciardi et al., 1996, 1998; Strayer and Smith, 1996; Strayer, 1999b).

Ohio has a history of studies of mussel population declines and regional losses of species richness. For instance, Hoggarth (1990) examined the Chagrin River of Northeastern Ohio and found that few species remained since the original northeastern Ohio survey work by Dean (1890). This suggests that the outlook for freshwater mussels is bleak, underscoring the need for well-cataloged historical collections. Because of the dire nature of the conservation status of freshwater mussels, collecting new specimens for ecological, conservation, and taxonomic studies is difficult and often impractical. Institutions such as natural history museums and universities that house unionid collections may represent the few remaining opportunities to study specimens. Museum collections of freshwater mussels may also be invaluable in reconstructing past unionid communities when published species lists are unavailable. The purpose of this paper is to make available the extensive freshwater mussel holdings at The Cleveland Museum of Natural history (CMNH) to facilitate future use of the specimens.

This paper lists the taxa in the collection as well as the CMNH catalog number, the number of lots and specimens, the states and years of collection, and the federal and Ohio endangered status. In some cases, older specimens do not have complete collection data (i.e., a date of collection). However, using archived information on the collectors and/or donors, a reasonable estimated range of years was determined. Because many of these specimens are >50 years old, they represent important historical records for their localities.

Results and Discussion

The CMNH collection of Unionida consists of 5123 specimens in 1452 lots, and 110 species from 5 families; 37 species are listed as species of special interest, threatened, endangered, or extirpated in Ohio. Nine specimens in three lots represent the tubercled blossom (*Epioblasma torulosa torulosa*, Fig. 1), three specimens from one lot represent the scalleshell (*Leptodea leptodon*), and three specimens in two lots represent the rock pocketbook (*Arcidens confragosus*), which have been extirpated from Ohio. Ten species are listed as federally endangered (<http://www.fws.gov>). Although

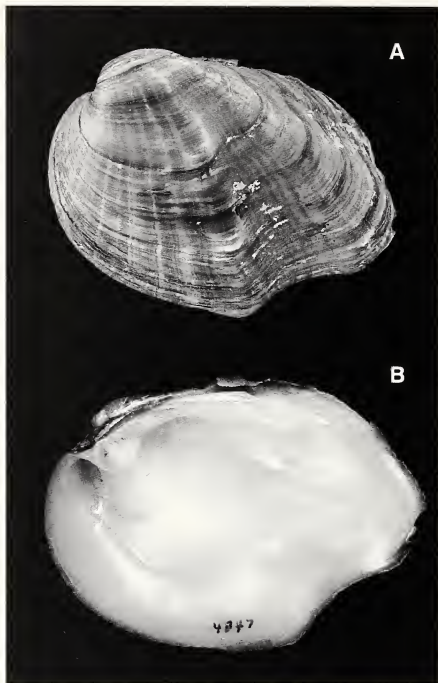


Figure 1. The tubercled blossom, *Epioblasma torulosa torulosa* (Rafinesque, 1820), currently extirpated from Ohio; A, shell exterior (maximum length = 6.0 cm); B, shell interior.

new specimens continue to be deposited in the collection, most species are represented from collections made > 50 years ago. Forty species are at least partially represented by specimens >100 years old (Appendix). Considering the current extreme loss of habitat and the reduction in unionid species distribution, natural history collections become invaluable for reconstructing historical distributions, and for studying species when it is impractical or impossible to collect and sacrifice new specimens.

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Appendix. List of freshwater mussels currently cataloged at The Cleveland Museum of Natural History (CMNH). The species, CMNH catalog number, number of lots and specimens, Ohio and federal endangered codes, and states and years of collection are given. Nomenclature follows that of Cummings and Mayer (1992) and Stansbery and Borror (1999). Ohio endangered codes: 1 = endangered, 2 = threatened, 3 = special concern, 4 = extirpated. Federal endangered code: E = federally endangered.

	CMNH catalog number	Lots	Count	Endangered codes		
Taxa				Ohio	Federal	States (years)
MARGARITIFERIDAE						
(MARGARITIFERINAE)						
<i>Margaritifera falcata</i> (Gould, 1850)	0101-01	3	5			OR (1901–02)
<i>M. margaritifera</i> (Linnaeus, 1758)	0101-01	4	13			CT (1930); MA (1978); ME (1902, 1905)
<i>M. marrianae</i> Johnson, 1983	0101-01	2	4			AL (1909, 1952)
UNIONIDAE (ANODONTINAE)						
<i>Alasmodonta heterodon</i> (Lea, 1829)	0201-08	4	11		E	CT (1940); MD (1913); VA (1901); VT (1901)
<i>A. marginata</i> Say, 1818	0201-08	13	40			IA (1954); MD (1908); OH (1902, 1927, 1930, 1940, 1951–1955, 1999)
<i>A. undulata</i> (Say, 1817)	0201-08	9	17			CT (1940); DC (1901–02); MA (1941); MD (1910); PA (1930); VA (1902)
<i>A. varicosa</i> (Lamarck, 1819)	0201-08	3	7			MD (1901–02, 1914)
<i>A. viridis</i> (Rafinesque, 1820)	0201-08	6	15			CT (1940); MI (1909); OH (1943, 1952)
<i>Anodonta californiensis</i> Lea, 1852	0201-02	1	10			CA (1954)
<i>A. nuttalliana</i> Lea, 1838	0201-02	2	3			CA (1901, 1916)
<i>A. suborbiculata</i> Say, 1831	0201-02	2	4	3		IL (1892)
<i>Anodontoides ferussacianus</i> (Lea, 1834)	0201-05	10	27			IN (1949); OH (1931, 1939–40, 1942–43, 1952–53, 1982)
<i>Arcidens confragosus</i> (Say, 1829)	0201-10	2	3	4		IA (1902); IL (1952)
<i>Lasmigona c. complanata</i> (Barnes, 1823)	0201-13	19	47			MI (1909); OH (1936, 1939, 1949, 1952, 1955)
<i>L. compressa</i> (Lea, 1829)	0201-13	7	10			GA (1930); MI (1905); OH (1935–36, 1951–52)
<i>L. costata</i> (Rafinesque, 1820)	0201-13	60	134			IA (1917); MI (1905, 1909, 1912); OH (1927, 1938–41, 1943–44, 1949, 1951–56); TN (1952)
<i>L. subviridis</i> (Conrad, 1835)	0201-13	2	15			FL (1870); NY (1952)
<i>Pyganodon cataracta cataracta</i> (Say, 1817)	0201-04	12	25			CT (1930, 1940); DC (1902); MD (1913); ME (1930); PA (1940); VA (1903, 1905)
<i>P. c. marginata</i> (Say, 1817)	0201-04	1	2			DC (1902)
<i>P. grandis grandis</i> (Say, 1829)	0201-04	83	209			IA (1954); LA (1943); MI (1909, 1912, 1949); OH (1935–36, 1938–42, 1945, 1949–56, 1967, 1977, 1998–1999); TX (1930, 1951); WI (1940)
<i>Simpsonia ambigua</i> (Say, 1825)	0201-12	1	1	3		OH (1952)
<i>Strophitis undulatus tennesseensis</i> Frierson, 1927	0201-07	1	1			TN (1940)

Taxa	CMNH catalog number	Lots	Count	Endangered codes		States (years)
				Ohio	Federal	
<i>S. u. undulatus</i> (Say, 1817)	0201-07	52	131			CT (1940); DC (1901); MD (1913); MI (1905,1909, 1912); OH (1902,1921,1927, 1936,1939–41, 1943–44, 1949–55,1978)
<i>Utterbackia imbecillis</i> (Say, 1829)	0201-03	7	30			MD (1936); OH (1941,1952,1954)
AMBLEMIDAE (AMBLEMIDAE)						
<i>Amblema plicata plicata</i> (Say, 1817)	0301-07	82	188			AR (1929,1931); IA (1954); IL (1902); IN (1902); KY (1950); MI (1905,1908–09, 1912,1949,1953); NY (1952); OH (1902, 1927,1931,1938–40,1943, 1949, 1951–55, 1967); TN (1865); TX (1901, 1951,1954)
<i>Canthyrina collina</i> (Conrad, 1837)	0301-16	1	1			VA (1940)
<i>C. spinosa</i> (Lea, 1836)	0301-16	2	3			GA (1910); MD (1917)
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)	0301-10	13	25	3		KY (1950); MI (1905,1912,1940); OH (1939–40,1951, 1954–1955); TN (1940)
<i>Elliptio buckleyi</i> complex (Lea, 1843)	0301-15	2	10			FL (1902,1928)
<i>E. complanata</i> (Lightfoot, 1786)	0301-15	56	567			CT (1930,1938,1940); DC (1901–02); GA (1902); MA (1900); MD (1900–1902, 1907–08, 1910, 1913–15); NH (1952,1956); NY (1905,1909,1921, 1952); OH (1936); VA (1903, 1905)
<i>E. congarea</i> (Lea, 1831)	0301-15	1	1			GA (1940)
<i>E. crassidens crassidens</i> (Lamarck, 1819)	0301-15	3	3	1		IN (1902); OH (1930); TN (1930)
<i>E. dilatata</i> (Rafinesque, 1820)	0301-15	45	147			AR (1952); KY (1941,1950); MI (1905,1909, 1925, 1949, 1953); OH (1927,1936–37, 1939,1944, 1949–56, 1999); TN (1930)
<i>E. downiei</i> (Lea, 1858)	0301-15	1	3			GA (1956)
<i>E. fisheriana</i> (Lea, 1838)	0301-15	7	29			DC (1902); MD (1900,1907); VA (1903, 1905)
<i>E. fisheriana</i> complex (Lea, 1838)	0301-15	1	4			NC (1906)
<i>E. hopetonensis</i> (Lea, 1838)	0301-15	1	1			GA (1940)
<i>E. lanceolata</i> (Lea, 1827)	0301-15	1	1			CT (1930)
<i>Fusconaia ebena</i> (Lea, 1831)	0301-09	4	7	2		KY (1950); OH (1930); TN (1940)
<i>F. flava</i> (Rafinesque, 1820)	0301-09	37	162			MI (1949,1953,1956); OH (1902,1924, 1930–31, 1943, 1949,1951,1953–55); TN (1865); WI (1930)
<i>F. maculata maculata</i> (Rafinesque, 1820)	0301-09	12	24	1		KY (1941); OH (1927,1940,1953–55)
<i>Gonidea angulata</i> (Lea, 1838)	0301-20	1	6			CA (1908)
<i>Hemistena lata</i> (Rafinesque, 1820)	0301-19	1	1	1	E	OH (1940)
<i>Lexingtonia dolabelloides</i> (Lea, 1840)	0301-11	1	1			TN (1865)
<i>Megaloniais boykiniana</i> (Lea, 1840)	0301-01	2	2			FL (1952); GA (1952)

Taxa	CMNH catalog number	Lots	Count	Endangered codes		States (years)
				Ohio	Federal	
<i>M. n. nervosa</i> (Rafinesque, 1820)	0301-01	7	9	1		IN (1902); KY (1950); TN (1940); TX (1951,1954)
<i>Plectomerus dombeyana</i> (Valenciennes, 1827)	0301-03	2	4			TX (1954,1957)
<i>Plethobasus cicatricosus</i> (Say, 1829)	0301-12	1	1	1	E	TN (1940)
<i>P. cyphus</i> (Rafinesque, 1820)	0301-12	2	3	1		OH (1955); TN (1930)
<i>P. striatus</i> (Rafinesque, 1820)	0301-12	3	5			OH (1930); TN (1865,1940)
<i>Pleurobema clava</i> (Lamarck, 1819)	0301-13	8	15	1	E	IL (1905); IN (1904,1944); OH (1927, 1949, 1952); TN (1910)
<i>P. cordatum</i> (Rafinesque, 1820)	0301-13	5	7	1		IN (1956); KY (1950); OH (1912,1930,1940)
<i>P. plenum</i> (Lea, 1840)	0301-13	2	2	1	E	IL (1905); TN (1940)
<i>P. rubrum</i> (Rafinesque, 1820)	0301-13	3	6	1		IN (1956); OH (1930,1954)
<i>P. sintoxia</i> (Rafinesque, 1820)	0301-13	27	60	3		IL (1930); MI (1905,1949,1953); OH (1927,1943, 1953-1955)
<i>Quadrula apiculata apiculata</i> (Say, 1829)	0301-06	1	2			TX (1902)
<i>Q. asperata asperata</i> (Lea, 1861)	0301-06	1	1			TX (1954)
<i>Q. cylindrica cylindrica</i> (Say, 1817)	0301-06	11	20	1		AR (1958); IN (1902,1952); OH (1927, 1940, 1951, 1953-55)
<i>Q. metanevra</i> (Rafinesque, 1820)	0301-06	2	2	1		AL (1954); TN (1940)
<i>Q. nodulata</i> (Rafinesque, 1820)	0301-06	3	4	1		IL (1902); KY (1950); OH (1940)
<i>Q. pustulosa pustulosa</i> (Lea, 1831)	0301-06	27	50			IA (1954); MI (1909,1949); MO (1901); KY (1950); OH (1940,1951,1953-55); TN (1862,1869,1940)
<i>Q. quadrula</i> (Rafinesque, 1820)	0301-06	19	34			IL (1958); KY (1950); MI (1909); OH (1951,1953-55, 1958,1967)
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	0301-04	27	75			AL (1954); AR (1939); IA (1902); IL (1902); IN (1902); OH (1927,1930,1951,1953-55); TN (1940); TX (1954)
<i>Uniomorus tetralasmus</i> (Say, 1831)	0301-22	1	2	2		KS (1907)
AMBLEMIDAE (LAMPSILINAE)						
<i>Actinonaias ligamentina ligamentina</i> (Lamarck, 1819)	0302-07	29	66	4		AR (1952); IN (1902); OH (1921,1935, 1940,1949, 1952-1955)
<i>A. l. orbis</i> Morrison, 1942	0302-07	1	1			TN (1940)
<i>Cyprogenia aberti</i> (Conrad, 1850)	0302-03	1	1			AR (1958)
<i>C. stegaria</i> (Rafinesque, 1820)	0302-03	7	23	1	E	IL (1905); IN (1898,1902); OH (1951, 1954-55)/TN (1930)
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	0302-08	5	13	1		IA (1956); OH (1940,1952-53); TN (1930)

Taxa	CMNH catalog number	Lots	Count	Endangered codes		States (years)
				Ohio	Federal	
<i>Epioblasma biemarginata</i> (Lea, 1857)	0302-20	1	1			TN (1910)
<i>E. brevidens</i> (Lea, 1831)	0302-20	1	2		E	TN (1865)
<i>E. rangiana</i> (Lea, 1838)	0302-20	1	2			IL (1905)
<i>E. torulosa torulosa</i> (Rafinesque, 1820)	0302-20	3	9	4	E	IL (1905); OH (1956); TN (1865)
<i>E. triquetra</i> (Rafinesque, 1820)	0302-20	17	90	2		OH (1940–41,1943,1951,1953–54,1958)
<i>Glebulula rotundata</i> (Lamarck, 1819)	0302-06	1	1			TX (1910)
<i>Lampsilis cariosa</i> (Say, 1817)	0302-19	11	44			DC (1902); MD (1901,1916,1952); NY (1935); TX (1954); VA (1940)
<i>L. dolabraeformis</i> (Lea, 1830)	0302-19	1	2			GA (1953)
<i>L. fasciola</i> Rafinesque, 1820	0302-19	4	8	3		IN (1902,1952); OH (1953–54)
<i>L. ovata</i> (Say, 1817)	0302-19	11	47	1		MI (1909); OH (1940,1951,1953–55); TX (1940)
<i>L. radiata hydiana</i> (Lea, 1838)	0302-19	1	4			TX (1954)
<i>L. r. luteola</i> (Lamarck, 1819)	0302-19	169	745			IA (1917); IL (1902); MI (1902,1905, 1909, 1912, 1949–50,1953); NY (1949–50); OH (1902,1921, 1924, 1927, 1935–36, 1938–41, 1943–45,1949–56, 1958–59, 1967,1996); PA (1949); VA (1940)
<i>L. r. radiata</i> (Gmelin, 1791)	0302-19	23	118			DC (1900–02,1910,1912); FL (1940); MD (1905); NH (1952); OH (1953,1955); PA (1940); VA (1901, 1903, 1905,1930)
<i>L. saturata</i> (Lea, 1852)	0302-19	1	1			TX (1954)
<i>L. splendida</i> (Lea, 1838)	0302-19	1	2			TN (1940)
<i>L. teres teres</i> (Rafinesque, 1820)	0302-19	2	7	1		IA (1956); TX (1954)
<i>L. ventricosa</i> (Barnes, 1823)	0302-19	111	350			IA (1954); IL (1902); KY (1952); MI (1905,1912, 1949–1950, 1952–53); NY (1902); OH (1927, 1930–31, 1935–36, 1938–39,1941–1944,1949, 1951–56, 1958, 1967); VT (1902)
<i>Leptodea fragilis</i> (Rafinesque, 1820)	0302-11	58	315			AL (1913); IN (1902); MI (1949–50,1953, 1956); OH (1937,1940–41,1943,1950, 1953–54, 1956, 1958, 1967); TX (1954)
<i>L. leptodon</i> (Rafinesque, 1820)	0302-11	1	3	4		OH (1930)
<i>L. ochracea</i> (Say, 1817)	0302-11	2	6			PA (1940); VA (1940)
<i>Ligumia nasuta</i> (Say, 1817)	0302-15	37	96	1		DC (1902); MD (1903); MI (1949,1953); NC (1906); NY (1952); OH (1930,1940, 1949, 1953–55); TX (1910, 1951, 1956); VA (1901,1905)
<i>L. recta</i> (Lamarck, 1819)	0302-15	27	106	2		IA (1952); MI (1940,1950,1952); OH (1912,1949, 1952–56,1967)
<i>Obliquaria reflexa</i> Rafinesque, 1820	0302-02	17	50	2		AL (1956); IL (1902,1910); MI (1949–50, 1953); OH (1954,1967); TN (1940); TX (1954)

Taxa	CMNH catalog number	Lots	Count	Endangered codes		States (years)
				Ohio	Federal	
<i>Obovaria olivaria</i> (Rafinesque, 1820)	0302-09	2	2	1		KY (1950); TN (1940)
<i>O. retusa</i> (Lamarck, 1819)	0302-09	4	8	1	E	OH (1910); TN (1910,1921,1940)
<i>O. subrotunda</i> (Rafinesque, 1820)	0302-09	8	26			OH (1925,1940-41,1943,1954); TN (1940)
<i>Potamilus alatus</i> (Say, 1817)	0302-12	85	453			IL (1952); IN (1902); MI (1949-50,1953, 1956); NY (1949); OH (1869,1924,1937, 1940, 1943,1949, 1952-56,1958,1967, 1979,1999)
<i>P. amphichaenus</i> (Frierson, 1898)	0302-12	1	5			TX (1954)
<i>P. purpuratus</i> (Lamarck, 1819)	0302-12	3	4			TX (1951,1954)
<i>Psychobranchus fasciolaris</i> (Rafinesque, 1820)	0302-01	29	86			MI (1909,1953); OH (1927,1943,1949-51, 1953-55); TN (1940)
<i>P. greeni</i> (Conrad, 1834)	0302-01	1	2		E	AL (1952)
<i>P. occidentalis</i> (Conrad, 1836)	0302-01	3	6			AR (1952)
<i>P. subtentum</i> (Say, 1825)	0302-01	1	2			TN (1956)
<i>Toxolasma paulus</i> (Lea, 1840)	0302-13	1	1			FL (1909)
<i>T. parvus</i> (Barnes, 1823)	0302-13	1	1			OH (1951)
<i>Truncilla donaciformis</i> (Lea, 1828)	0302-10	10	87	2		IA (1956); MI (1949); OH (1943,1954-55)
<i>T. truncata</i> Rafinesque, 1820	0302-10	14	45	3		AR (1956); IL (1910); IN (1902); MI (1949, 1953); OH (1954-56); TN (1940)
<i>Villosa amygdala</i> (Lea, 1843)	0302-18	2	8			FL (1902)
<i>V. fabalis</i> (Lea, 1831)	0302-18	3	6	1		MI (1949); OH (1940,1951)
<i>V. iris iris</i> (Lea, 1829)	0302-18	7	14			MI (1912); OH (1949,1952-53,1996,1999); WI (1940)
HYRIIDAE (HYRIINAE)						
<i>Diplodon charruanus</i> (d'Orbigny, 1835)	0401-07	1	2			VA (1940)
TOTALS		1452	5123			

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NOTE

FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) OF THE OHIO & ERIE CANAL, CUYAHOGA VALLEY NATIONAL PARK, OHIO

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Freshwater mussels (Bivalvia: Unionidae) have become established in canals in Ohio and the eastern United States in addition to their indigenous habitat of permanent natural lakes and streams. For example, Higgins (1858, p. 550) noted the following for the Columbus feeder canal of the Ohio & Erie Canal: "Many species have traversed the whole length of the canal, and many species there thrive and become abundant which are quite rare in the adjacent rivers." Sterki (1907) suggested that the unionid species *Elliptio complanata* (Lightfoot) may have gained access to the Tuscarawas River from Lake Erie via the Ohio & Erie Canal, although Barber (1982) suggests other avenues of dispersal. In addition, it was observed that the stillwater species *E. complanata*, *Strophitus undulatus* (Say), and *Utterbackia imbecillis* (Say) "seem to thrive" in parts of the canal in the Chesapeake & Ohio Canal National Historical Park, Maryland (Anonymous, 1998). Nevertheless, published information on the unionid populations of canals in the United States is scarce. For northeastern Ohio, Smith (2000) and Smith et al. (2002) reported that sections of the Ohio & Erie Canal located within the Cuyahoga Valley National Park supported a thriving freshwater mussel population composed of the species *Pyganodon grandis* (Say) and *Toxolasma parvus* (Barnes). The canal, which is normally difficult to survey for mussels because of steep banks, vegetative cover, and a soft, muddy substrate, had been drained locally during the summer of 1998 for repairs, revealing a large population of

recently dead and dying mussels. Eight hundred fourteen *P. grandis* and 48 *T. parvus* were counted in a 2.4 km long section of dry canal bed (Figure 1).

Sections of the canal were drained again, during the summer of 2000, for a construction project involving the Tinkers Creek aqueduct where it crosses the canal. From June 16 through July 17, a 3.3 km long section of dry canal bed with an area of approximately 33,000 m² was visually surveyed to provide new data on mussel occurrence. The surveyed area of the canal extended from the northern boundary of the Cuyahoga Valley National Park, at Rockside Road, to the Tinkers Creek aqueduct (Figure 1). This survey revealed the presence of 838 *P. grandis*, 11 *T. parvus*, and 2 *U. imbecillis*, all freshly dead or dying. Of these, 20 *P. grandis* and 3 *T. parvus* were found as part of a "middened accumulation" left behind by an animal. The midden was associated with what appeared to be a muskrat burrow and was located about 1 m above the canal bottom on the east bank, roughly 1 km south of Rockside Road. The species *U. imbecillis*, while rare in the canal, is more common in lakes in the lower Cuyahoga River valley (Smith, 2000; Smith et al. 2002) and within the Cuyahoga River in its upper reaches (Huehner, 1985; Hoggarth, 1990).

Freshwater mussels ("*Unio*") were reported from the Ohio & Erie Canal as early as the 1830s. Wied-Neuwied (1906, p. 150) described the following for late June, 1834: "After we left Circleville we saw, on the canal, a great num-

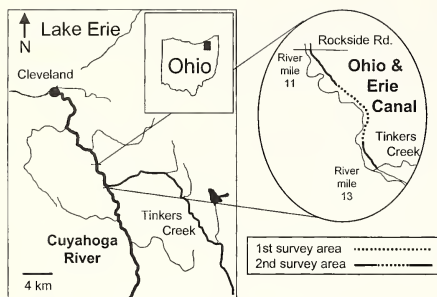


Figure 1. The lower Cuyahoga River and its tributaries, including Tinkers Creek. The search region of the Ohio & Erie Canal (magnified for detail) covers the portion of the canal that parallels the river between river mile 11 and river mile 13, as measured from the mouth of the Cuyahoga River at Lake Erie.

ber of shells (*Unio*), of a greenish color, with darker stripes, which were very frequent here; most of them were floating without the animal, which was, however, found dead in some of them." The species he described is likely *P. grandis*, which has the vernacular name of "giant floater." This species colonized the canal almost immediately, because the northern segment of the canal originating at Cleveland was opened in July, 1827, and the section around Circleville was opened in October, 1831 (Scheiber, 1969, p. 51). Other historical information on the mussel fauna of the canal includes a report by Dean (1890) of the occurrence of the species *Lasmigona complanata* (Barnes).

These recent and historical data have the following implications: First of all, the Ohio & Erie Canal has long been a viable habitat for mussels. In addition, the species inhabiting the canal may have changed in response to the canal being a more loticlike habitat during its period of usage, and then becoming a more lenticlike habitat in its abandonment. For example, *L. complanata* is a typical riverine species and inhabits upper reaches of the Cuyahoga River today, but no longer the canal. Moreover, *P. grandis* and *U. imbecillis* also occur in lakes and ponds within the national park, although the former apparently colonized the canal shortly after it opened. *Toxolasma parvus* has been observed only in the canal within the national park, although two spent, disarticulated valves were reported from the upper reaches of Tinkers Creek outside of the park boundaries by Krebs et al. (2002). Finally, this study demonstrates that the canal provides habitat for abundant mussel populations within the Cuyahoga Valley National Park. Therefore, careful management of the canal will assure their continued existence in the park.

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TRIGONOCARPUS EXCRESCENS JANSSEN, 1940, A SUPPOSED SEED FROM THE PENNSYLVANIAN OF ILLINOIS, IS A MILLIPED (DIPLOPODA: EUPHOBERIIDAE)

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ABSTRACT

The syntype specimens of *Trigonocarpus excrecens* Janssen, 1940, do not belong to the form genus *Trigonocarpus* Brongniart, 1828, but are composed of body segments of euphoberiid millipeds. Some other specimens described as plants by Janssen also may be fossil arthropod parts.

Introduction

Fossil myriapods have been confused with other types of organisms, including annelid worms, onychophorans, arachnids, crustaceans, and ferns (see Hannibal, 2001, for examples and citations). Such misidentifications are due to the superficial resemblance of whole or partial myriapod fossils to fossils of other organisms, and vice versa. The purpose of this note is to redescribe and discuss the syntype specimens of *Trigonocarpus excrecens* Janssen, 1940. These supposed plant specimens are composed of body segments of euphoberiid millipeds.

Specimens referred to are in the collections of the Illinois State Museum (ISM), The Cleveland Museum of Natural History (CMNH), the Field Museum of Natural History (FMNH), and the Yale Peabody Museum (YPM). Terminology follows Burke (1979) and Hannibal (1995, 1997a).

Systematic Paleontology

Class DIPLOPODA Blainville in Gervais, 1844

Subclass HELMINTHOMORPHA Pocock, 1887

Order EUPHOBERIIDA Hoffman, 1969

Family EUPHOBERIIDAE Scudder, 1882

Genus MYRIACANTHERPESTES Burke, 1979

MYRIACANTHERPESTES EXCRESCENS (Janssen), new combination

Figures 1–2

Trigonocarpus excrecens JANSSEN, 1940, p. 100–101, Pl. 28, figs. 3–4; LANGFORD, 1958, p. 312, figs. 584, 585; LEARY, 1976, p. 58–59; GASTALDO AND MATTEN, 1978, table 2 (p. 887).

Material

Cotypes (syntypes), ISM 14764a/b (14764b is illustrated in Figure 1A and in Janssen 1940, Pl. 28, fig. 3; a latex cast of 14764a is illustrated in Figure 2A) and ISM 14765a/b (14765a is illustrated in Figure 1B and in Janssen, 1940, Pl. 28, fig. 4; a latex cast of 14765b is illustrated in Figure 2B). Both specimens are from a strip mine in Will Co., Illinois. They are preserved in typical Mazon-Creek type siderite concretions ("ironstone nodules"), in part and counterpart, from the Francis Creek Shale Member (Pennsylvanian, Westphalian D) of the Carbondale Formation. These were the only specimens known to Janssen at the time he wrote his 1940 paper. Latex casts were made from prepared natural molds of the specimens (see Hannibal "2000," p. 23–24, for details).

Diagnosis

Large eupheriid millipeds with relatively long lateral spines having prominent, curved anterior prongs; long, simple, stout, diverging paramedian spines; and anterior and posterior spinelets.

Description of Specimens

Portions of large eupheriids in dorsal view. Composed of two to three body segments. Width of segments, excluding lateral spines, up to about 23 mm. Prozonites and metazonites distinct. Paramedian spines long, stout, outwardly directed and gently diverging.

ISM 14765a/b, larger and more complete specimen (Figures 1B, 2B), 22 mm long, consisting of portions of three body segments; prozonite and metazonite of two body segments present, only metazonite of third segment present. Width of best preserved segment 23 mm; length of best preserved metazonite 6.7 mm. Body segments overlap. Prominent paramedian spines, up to about 5.4 mm long (as determined from latex of counterpart, Figure 2B), simple, stout, diverging, and borne on stout anterior ridge of metazonite. Lateral tubercle (bearing ozopore?) present. Lateral spine stout, curved towards posterior, 16.8 mm long, 3.5 mm wide just before base of anterior prong originates. Anterior prong of lateral spine stout, curved, 6.5 mm long. Posterior prong 8.4 mm long. Anterior spinelet poorly preserved, curved posteriad, 5.2 mm long. Posterior prong slightly curved, 5.0 mm long.

Less complete specimen, ISM 14764a/b (Figures 1A, 2A), 18.7 mm long, consisting of two segments; prozonite and metazonite of one segment present; most of other preserved segment consisting of metazonite. Width of best preserved segment 18 mm; length of anterior metazonite about 9 mm measured along midline. Body segments overlap. Prominent paramedian spines, > 3.6 mm long, simple, stout, gently and outwardly curving, and borne on stout anterior ridge of metazonite.

Remarks

The two specimens are similar in size and both bear similar paramedian spines. The spines appear to be of different lengths (Figure 2) as ISM 14765b (a natural mold) was more



Figure 1. *Myriacanthepestes excrescens* (Janssen, 1940), unwhitened syntypes preserved in concretions. A, ISM 14764b; B, ISM 14765a (paramedian spines appear as nodes; arrow points to lateral spine). Scale bar equals 1 cm.

completely prepared before latex casts were made. The latex casts of the paramedian spines are also somewhat distorted. The natural mold of ISM 14764 was not prepared as completely, as the material infilling the spines of this specimen was much denser than that filling the natural mold of ISM 14765. The paramedian spine on bottom right of specimen (Figure 2A) is more indicative of spine length as its mold was more easily prepared than the mold of the other spines.

Long lateral spines, one of which is seen on ISM 14765a/b (Figures 1B and 2B), and which can be seen in Janssen's figure (1940, Pl. 28, fig. 4), are diagnostic of the genus *Myriacanthepestes*, as is the presence of an anterior spinelet. Burke (1979, p. 1) referred five species to the genus *Myriacanthepestes*: *M. ferox* (Salter, 1863), *M. hystricosus* (Scudder, 1890a) (see also Scudder 1890b), *M. inequalis* (Scudder, 1890a) (see also Scudder 1890b), *M. clarkorum* (Burke, 1973); and *M. bradebirski* Burke, 1979. Burke (1979) provided diagnoses for two of these, *M. ferox* (p. 5–6) and *M. bradebirski* (p. 12), and supplied restorations of the diplosomites of *M. ferox* and *M. hystricosus*. The very long,

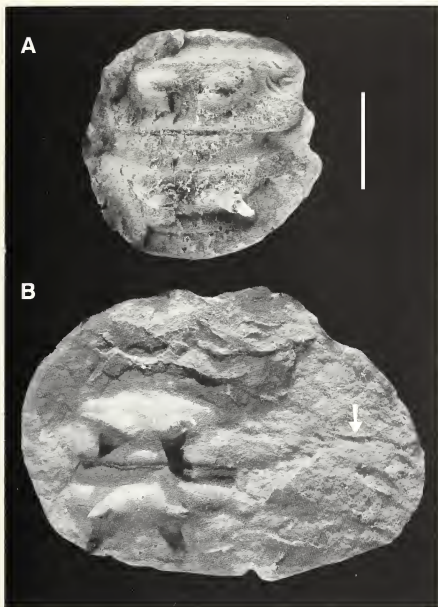


Figure 2. *Myriacanthepestes excrecens* (Janssen, 1940), latex casts of natural molds of the syntypes. A, latex cast of ISM 14764a (paramedian spine on bottom right is more indicative of spine length); B, latex cast of ISM 14765b (shadows cast by paramedian spines indicate their long length; arrow points to lateral spine). Scale bar equals 1 cm.

diverging, paramedian spines ("subdorsals" of Burke, 1979) of the specimens are closer to those of *M. ferox* (Burke, 1979, fig. 4), but they are shorter and less curved than those of *M. hystricosus* (Burke, 1979, fig. 1). However, the anterior prong of the lateral spine is more like that of *M. hystricosus* (Hannibal, 1997, Fig. 13.10) and not like that of *M. ferox* as diagnosed by Burke (1979, p. 5–7, fig. 4). The lateral spines of *M. excrecens* are much like those of *M. clarkorum*, but, according to Burke's (1973, p.1, fig. 1) diagnosis, *M. clarkorum* has paramedian spines ("subdorsals") reduced to nodes. It is possible, however, that the nodelike nature of the paramedian spines of *M. clarkorum* is preservational in nature. *Myriacanthepestes bradebirski* is a small species with a rounded, tapering lateral spine (Burke, 1979, p. 12–13). The lectotype of *M. inequalis* (Scudder, 1890a, Pl. 33, fig. 2) established by Burke (1979, p. 5), has very elongate, and rather slender, lateral spines, but its paramedian spines have not been described.

It is likely that *M. excrecens* will eventually prove to be a synonym of one of the already described euphoberiid species. The lack of a complete suite of preserved characters for the specimens referred to *M. excrecens*, and the incomplete nature of some of the descriptions of other species in the genus, make this a difficult task. A systematic revision of the genus *Myriacanthepestes*, and other euphoberiid genera, is needed.

Janssen (1940) misinterpreted the milliped segments of ISM 14764 and 14765 as valves of seeds in the genus *Trigonocarpus* Brongniart, 1828, which they do superficially resemble (see especially Figure 1A). The transverse ridges of the milliped segments vaguely resemble the longitudinal "ribs" and ridges of species of these seeds (see, for example, specimens figured in Hoskins and Cross, 1946). Their "oval" aspect is due to the slightly askew way that milliped segments may overlap. Janssen (1940) misinterpreted the paramedian spines on the metazonites as tubercles or spinelike excrescences. Langford's reconstruction of *T. excrecens* (1958, fig. 584, 4a), based on Janssen's interpretation, is erroneous, combining what are really three milliped body segments into a *Trigonocarpus*-like shape. The paired sets of nodes shown in his reconstruction, and seen on the specimens, are actually bases of paramedian spines. This is most clearly shown in latex casts (Figure 2).

Partially disarticulated euphoberiid exoskeletons have long been known (see, for example, Scudder, 1890, Pl. 25, figs. 1, 3). Concretions containing a small number of segments of euphoberiids are not uncommon, and examples can be found in most large museum collections of Mazon Creek concretions. The presence of two or three euphoberiid body segments in a concretion is merely part of a preservational continuum, with various numbers of preserved body segments found in concretions. Examples of euphoberiid fossils consisting of only a few segments in concretions include: FMNH PE 28724, consisting of a single euphoberiid segment; FMNH PE 16443, consisting of two segments; FMNH PE 25134, consisting of three segments; and CMNH 9190, consisting of parts of five segments. Segments may be articulated, or separate. YPM 9917, for example, consists of three euphoberiid body sections in a single concretion, one segment of which is separated from the others, and the other two (one of these a partial segment) are joined.

The other type specimens illustrated in Janssen's (1940) Pl. 28 and referred to *Carpolithus noëi* Janssen and, especially, to *Schopfia* Janssen, may also be misidentified; they may not be plants. At least some of the figured specimens of *Schopfia* Janssen, 1940, but especially ISM 14768 (Pl. 28, fig. 6) and ISM 14769 (Pl. 28, fig. 7) (see also Langford, 1958, figs. 664–668), as well as material Langford referred to as "seed attachments" (1958, p. 344, figs. 669–674) bear a resemblance to limb or other body parts of large Arthropoda such as *Arthropleura* (which is known from the Mazon Creek fauna). Langford (1958, p. 344) noted the lack of veins on specimens of *Schopfia*; indeed, specimens

referred to that genus lack definitive plant characters. The holotype of *S. calceola* Janssen (ISM 14769) resembles parts associated with *Arthropleura* (compare *S. calceola*, Janssen, Pl. 28, fig. 7 to the *Arthropleura* material figured in Hannibal, 1997b, fig. 5). While some or all of the specimens referred to *C. noëi* and *Schopfia* may well be arthropodan, they are not parts of euphoberiid diplopods.

Acknowledgments

One of us (SLM) first discovered that these specimens were, in fact, euphoberiids, and J. Almond, then with Cambridge University, first recognized that ISM 14765 belonged to the genus *Myriacanthepestes*. Access to type material and other aid was provided by R. Leary and J. Saunders, Illinois State Museum. Access to additional material was provided by R. White, Yale Peabody Museum, and G. Buckley and S. Lidgard, Field Museum of Natural History. Photographs of latex casts were taken and printed by B. Frumker and G. Petusky, The Cleveland Museum of Natural History. Photographs of the specimens were provided by G. Andrashko, Illinois State Museum. This article was improved by the comments of Richard Hoffman, Virginia Museum of Natural History, and an anonymous reviewer.

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SURVEY OF FISHES, AMPHIBIANS, AND REPTILES OF THE CONNEAUT CREEK DRAINAGE SYSTEM, ASHTABULA COUNTY, OHIO

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ABSTRACT

A survey of fishes, amphibians, and reptiles was conducted in the Ohio portion of the Conneaut Creek drainage system, Ashtabula County, during the years 1996–2003. Objectives of the survey were to determine the species composition of fishes, amphibians, and reptiles; to estimate their abundances; and to determine their respective geographic distributions within the Ohio portion of the watershed. Qualitative and quantitative occurrence data were compiled from multiple sources for 83 sites in two townships and one incorporated community. In all, 75 species of fishes plus two hybrid taxa, 19 species of amphibians, and 14 species of reptiles were documented for the watershed. Species richness and designated abundances at each site as well as occurrence and frequency of occurrence over all sites are presented. Drainage system records of 17 species of fishes and three species of reptiles were noted. The survey produced new township records for four species of amphibians and 11 species of reptiles. A record of *Sternotherus odorata* was documented for Ashtabula County. Three species of fishes previously known from the watershed were not encountered.

Introduction

Surveys of amphibians and reptiles are frequently done for political units such as counties or townships or for other usually smaller artificial units such as parks or natural areas. Data collected in these anthropogenic geographic units can easily be plotted on maps and used for referencing presence/absence, local abundance, and coarse-grained geographic distribution. Fish surveys often conform with this methodology but are conducted at easily accessible sites at disjunct locales, the data from which may be either coarse or fine grained. Fish data, however, are indicative of the species that live within the drainage system, typically a naturally occurring geomorphically and geographically defined entity.

Fine-grained data based upon many proximate sites provide a good temporal picture of the geographic distribution and abundance of species within that watershed and are often more useful for future environmental studies, assessments, and planning than coarse-grained data.

We conducted a survey to determine the species composition of fishes, amphibians, and reptiles; to estimate their abundances; and to determine their respective geographic distributions within the Ohio portion of the Conneaut Creek drainage system in Ashtabula County. To achieve those objectives, records were compiled from published reports, from the Ohio Environmental Protection Agency FINS (Fish Information Network System) database, from field survey

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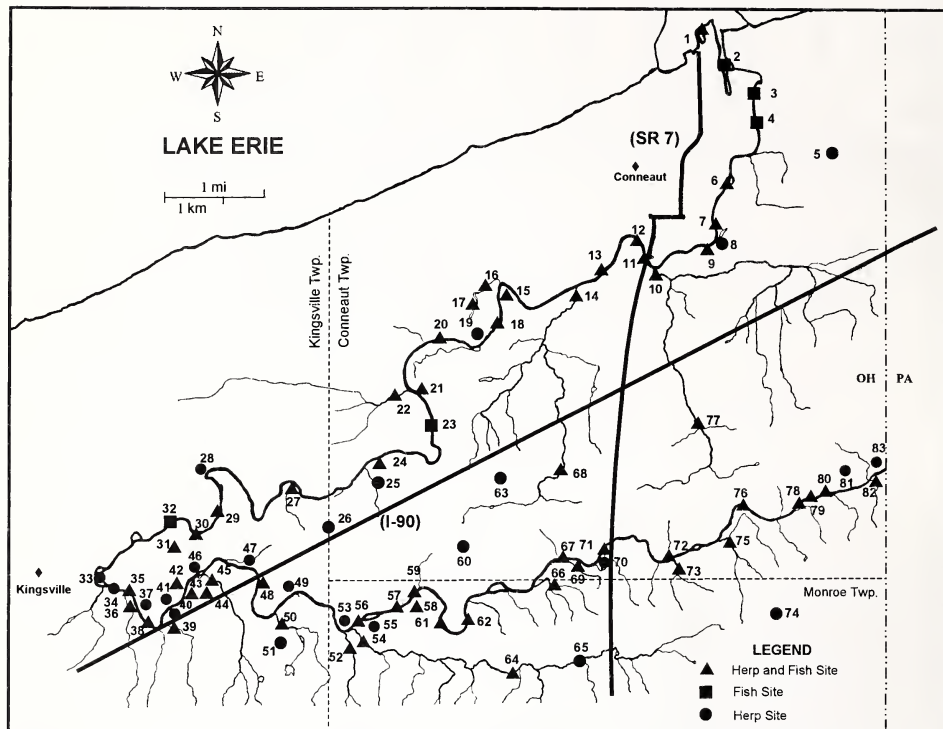


Figure 1. Map of the Ohio portion of Conneaut Creek drainage system showing 83 survey site locations.

reports conducted by the United States Fish and Wildlife Service, from the ichthyology and herpetology collections of the Cleveland Museum of Natural History, and from our extensive recent field surveys.

Site Description

The headwaters of Conneaut Creek are in northwestern Pennsylvania from where it courses westward into Ashtabula County, the most northeastern county of Ohio. Of its total drainage area of 495.2 km² (191.2 mi²), the lower 20 percent or 97.6 km² (37.7 mi²) is located in Ohio (Ohio Department of Natural Resources Division of Water, 1960). Conneaut Creek enters the Central Basin of Lake Erie through Conneaut harbor in the city of Conneaut, Ohio; it flows through Monroe and Kingsville townships and Conneaut Incorporated. Few 3rd order tributary streams drain into the Ohio portion. Most tributaries are either 1st or 2nd order, and

none have recognized names (USGS 7.5 minute series topographic maps: Conneaut 1996 and North Kingsville 1994).

Two physiographic sections are represented in Ashtabula County (Anderson, 1983; Brockman, 2002). The Erie Lake Plain Section (Brockman, 2002), a northeastern extension of the Huron-Erie Lake Plains of the Central Lowland Province, extends along Lake Erie as lake plain in a narrow zone approximately 5.6 km (3.5 mi) wide near Conneaut (White and Totten, 1979, p. 4). The Erie Lake Plain is bordered on the south by the Portage Escarpment (Brockman, 2002), a transitional belt approaching 4.8 km (3 mi) in width that increases in elevation to the south (White and Totten, 1979, p. 4). The Glaciated Allegheny Plateaus (Brockman, 2002), the western portion of the Appalachian Plateaus Province, rises above the Portage Escarpment to the south (White and Totten, 1979; White, 1982).

Pleistocene glacial deposition with concurrent and subse-



Figure 2. Conneaut Creek valley within the Portage Escarpment showing the steep Chagrin Shale northeast facing slope with two patches of snow remaining. Photograph taken 2 April 2003 on the forested flood-plain of site 38, The Cleveland Museum of Natural History Blakeslee Barrows Preserve.



Figure 3. Second order tributary stream of Conneaut Creek showing a cascading waterfall over Chagrin Shale and a closed canopy of deciduous trees and eastern hemlock. Photograph taken 2 April 2003 of the northwest facing slope at The Cleveland Museum of Natural History Hubbard preserve.

quent erosion have sculptured the current landscape. The Erie Lake Plain is in general flat, poorly drained, and mostly covered with lacustrine silts, sands, and gravels overlaying glacial tills. It is traversed by several beach ridges most of which are fragmented and breeched by eroding streams and/or wave action from higher, earlier glacial lake stages.

The Portage Escarpment bedrock is overlaid with a series of parallel end moraines (White and Totten, 1979). In far



Figure 4. Seasonal channel pond on the forested Conneaut Creek flood-plain. Photograph taken 2 April 2003 of the northwest facing slope at The Cleveland Museum of Natural History Hubbard preserve about 50 m east of mouth of the tributary stream of Figure 3.

northeastern Ohio, the Painesville Moraine lies on the upper part of the escarpment and is characterized by rolling topography with till hummocks reaching 9 m (30 ft) (White and Totten, 1979, p. 11). The Ashtabula Moraine lies north and parallel to the Painesville Moraine on the lower part of the escarpment. Knolls up to 9 m (30 ft) in elevation create rolling, hummocky topography (White and Totten, 1979, p. 11).

Conneaut Creek flows westward from Pennsylvania in the deep gorge separating the Painesville Moraine to the south and the Ashtabula Moraine to the north. About 1.1 km (0.7 mi) east of Kingsville the creek abruptly bends north (Figure 1) through a large gap in the Ashtabula Moraine and then flows eastward on the lake plain between the Ashtabula Moraine on the south and Arkona beach ridge on the north. Blockage of the old Conneaut Creek channel by ice with deposition of the Whittlesey beach ridge of sands and gravels forced Conneaut Creek eastward. The creek then flows eastward about 5.6 km (3.5 mi) where it breeches the Arkona beach ridge near Camp Peet and courses northeastward across the lake plain toward Lake Erie (White and Totten, 1979). Ohio tributaries to Conneaut Creek head either on the lake plain or on the escarpment.

The Conneaut Creek gorge (Figure 2) and the valleys of most 2nd and 3rd order streams are incised through the glacial deposits to expose and/or flow upon the underlying Chagrin Shale. Cascading falls, some in excess of 10 m high, over shale and siltstone bedrock are common (Figure 3). Siltstone slabs are common in stream channels and are often exposed on the valley slopes. Glacial erratics, in addition to cobble, gravel, sand, and silts derived from local rock, occur in sufficient quantities and arrays to produce

manifold habitats. Some 2nd and 3rd order streams that have morainic heads in forested areas and flow either entirely within the escarpment or partially on lake plain have water temperatures that seldom exceed 21°C, even in years with prolonged drought conditions and above normal ambient temperatures.

Channel-margin pools, abandoned flood-plain channel ponds (Figure 4), and perched seasonal terrace ponds are present within the Conneaut Creek valley. Several abandoned channel ponds support luxuriant aquatic vascular plant communities.

Geographically the Conneaut Creek watershed is located in the northeastern Ohio Lake Erie snowbelt. Cold westerly and northwesterly winter winds across an open Lake Erie are warmed, pick up moisture, and rise slowly from the beach at an elevation of about 208 m (571 ft) across the lake plain. From Cleveland eastward the winds are deflected upward rapidly over the escarpment where thermal decline produces increased precipitation, often in the form of snowfall. The elevation of the southern boundary of the Painesville Moraine approaches 275 m (900 ft; USGS Conneaut, Ohio 1996 topographic map). Climatic data recording stations between Cleveland at 235 m (770 ft) and the city of Ashtabula at 211 m (690 ft) on the lake plain and in Dorset about 12.8 km (8 miles) south of the Painesville Moraine on the Glaciated Allegheny Plateaus at 299 m (980 ft) indicate an increase in mean annual snowfall and precipitation with decreasing mean annual temperature from west to east (Midwest Regional Climate Center, Champaign, Illinois). These climatic conditions interact to produce environs that tend to be cool and moist and are indicative of those farther north.

Mixed hardwoods with eastern hemlock cover much of the flood plain of Conneaut Creek. Gorge slopes and valleys of the tributaries are cool, moist growing sites and eastern hemlock-hardwood forests with striped maple are widespread (Figure 3). Densely shaded, cool environments occur in most ravines of both the escarpment and lake plain.

Materials and Methods

Records of occurrence of taxa within the Conneaut Creek drainage system were compiled from multiple sources. Field survey records of lamprey were provided by the United States Fish and Wildlife Service and include species recorded during larval lamprey population censuses and those individuals of all age cohorts salvaged during lampricide application (unpublished data, U.S. Fish and Wildlife Service, Marquette Biological Station). Fish survey records were obtained from the Ohio Environmental Protection Agency FINS database (unpublished data, Ohio EPA). Published drainage records for fish were recorded from Trautman (1981). The fish collection of The Cleveland Museum of Natural History, which includes the Andrew White Collection originally at John Carroll University, provided

many specimens and much data. All specimens collected during the years of field survey by the CMNH were deposited in the fish and herpetology sections of the Museum's vertebrate collections.

Published township records of occurrence for anurans were compiled from Walker (1946), Pfingsten (1998), and Davis and Menze (2000); published township records for salamanders were obtained from Pfingsten and Downs (1989), Pfingsten (1998), and Pfingsten and Matson (2003); and published records of reptiles were obtained from Conant (1951) and Zemco (1974).

Intensive study of the fish, amphibians, and reptiles for the Ohio portion of Conneaut Creek watershed by the primary investigator began in 1996; it became a priority in 1999 and continued into April 2003. Nets were used to capture fish; 1.8 m and 3.7 m seines and 3.7 m and 7.3 m bag seines all having 0.47 cm mesh were used. Sites were seined and/or dip netted repeatedly during each visit until no additional species were netted.

Amphibians were surveyed through visual encounter, by overturning rocks, slabs, logs, and trash and by anuran call recognition. Sites were visited during several seasons and varying times of the day. Amphibians were captured by hand, by seining and dip-netting for larvae, by using modified cylindrical minnow traps and screened box traps (Heyer et al., 1994).

Reptiles were surveyed through encounter, by overturning objects laying on the ground, by trapping, and through road kill. Metal sheets were laid on the ground in various habitats at sites 37, 41, 42, and 58 to aide in attracting lizards and snakes. Baited funnel turtle traps with 0.75 m and 0.9 m diameter hoops and having 2.5 cm mesh were used to capture turtles.

Erythrocyte size was used to differentiate diploid from polyploid individuals of the *Ambystoma jeffersonianum* complex (Pfingsten and Downs, 1989; Uzzell, 1964). Recognition of the advertisement call served to separate male tetraploid *Hyla versicolor* from diploid *H. chrysoscelis* (Matson, 1990); erythrocyte size (Matson, 1990) and geographic distribution (Pfingsten, 1998; Davis and Menze, 2000) were used to differentiate their tadpoles.

Amphibians and fishes were salvaged at various sites during and within a day following application of the lampricide TFM (3-trifluoromethyl-4-nitrophenol) in 1986, 1991, 1995, 2000 and in 2003 by museum staff and field survey personnel from several state and federal agencies.

Geographical longitudinal and latitudinal coordinates for each site are listed in Appendix 1. Site numbers in the appendices reference those plotted on the drainage system map of Figure 1. Where appropriate, a descriptive locality name is given for a site to facilitate positioning on a topographic map.

This survey did not include man-made backyard ponds created for home owner fire insurance coverage or farm

ponds typically stocked with largemouth black bass, sunfish, and channel catfish. These ponds generally provide suitable habitat for a repetitive and predictable array of amphibian and reptile species.

The number of individuals of each taxon encountered at each site during each visit was recorded and was later used to assign an abundance designation to each taxon at that site. The abundance of a species at a site is a subjective evaluation by the principle investigator and reflects the number of individuals over all life stages observed per visit and summed over all visits to the sites using all methodologies. No attempt was made to standardize sampling effort as that would have been counter productive because all vertebrate classes surveyed were sampled simultaneously and all available habitats were included. Some sites were surveyed once whereas others were visited as many as 11 times. The status designations assigned to each species or taxon recorded are as follows:

abundant — numerous and widespread within the site (high density with high frequency of encounter).

common — present at many localities within the site (low to moderate densities with moderate frequency of encounter).

uncommon — present at few localities within the site (low to moderate densities with low frequency of encounter).

rare — few individuals present at restricted localities (very low density with very low frequency of encounter).

present — only one individual of the taxon was vouchered with no quantitative assessment of the number of individuals encountered at the site during a single survey; the assignment of an abundance designation seems premature.

present () — the taxon was represented by tadpoles (T), larvae (L), or eggs (E) only.

— the number of individuals of a taxon recorded at a site was low, and we considered the data insufficient to accurately assign an abundance designation.

A-R (#) — the site was surveyed more than once and sufficient data were available to assign an abundance designation. This form of designation was used for amphibian taxa that utilize only one medium (aquatic or terrestrial; e.g., *Necturus* and *Plethodon*, respectively) where larvae, juveniles, and adults have similar probabilities of encounter using the same search methodologies. It was also applied to reptiles that often occur in relatively low numbers even when common because of their higher trophic status. The quantitative data should facilitate future comparisons.

Some species of fish occur only in the tributaries, others

occur only in the main creek, whereas others occur in both stream categories. An abundance designation does not necessarily indicate equal numbers of individuals encountered when applied to different taxa or to the same taxon when found in both tributaries and Conneaut Creek.

The occurrence, the total number of sites at which a taxon was recorded, and the frequency of occurrence (*f*) in percent were calculated as a means of censusing taxa over all appropriate sites (Smith and Smith, 2001). This method is merely an indicator for comparative purposes because sites were of unequal size and the times spent searching sites were not equal. The total number of fish sites used in the frequency calculation was 59 whereas the number of amphibian/reptile sites was 77.

Binomial names and common names of fishes used are in accordance with those of the American Fisheries Society (Robins et al., 1991); names of amphibians and reptiles used are those published by the Society for the Study of Amphibians and Reptiles (Crother, 2001) with one exception. The name *Ambystoma platineum* (Silvery Salamander) was conserved (Frost, 1985) to refer to the triploid member of the *A. jeffersonianum* complex having the unisexual biotype JLL (Petranka, 1998, p. 124). Taxa not included in appendices are authored in the text.

Results and Discussion

Data compiled from all sources represent 83 different survey sites (Figure 1; Appendix 1) within the Conneaut Creek drainage system. Among those sites, 53 were surveyed for fishes, amphibians, and reptiles; 24 were only surveyed for amphibians and reptiles (no fish were present); and 6 were only surveyed for fishes. The fish community included 75 species plus two hybrid taxa (Appendix 2), whereas the herptofaunal community included 19 species of amphibians and 14 species of reptiles (Appendix 3).

Fish

Three species of fishes, the hornyhead chub (*Noemigobius biguttatus* (Kirtland, 1840)), the common shiner (*Luxilus cornutus* (Mitchill, 1817)), and the eastern sand darter (*Ammocrypta pellucida* (Putnam, 1863)), mapped in Trautman (1981, p. 269, 341, 648, respectively) as occurring within the Conneaut Creek drainage system were not detected during our field surveys. The striped shiner (*L. chryscephalus*) was widespread in both the tributaries and Conneaut Creek; because of its similarity in appearance to the common shiner (*L. cornutus*) it is feasible that the common shiner was overlooked. However, neither our field surveys nor those conducted by Ohio EPA detected the common shiner, and collection records for this taxon in the drainage precede 1955 (Trautman, 1981). Similarly, collection records for the hornyhead chub and the eastern sand darter in the drainage are prior to 1924 (Trautman, 1981, p. 269 and 648).

These species may be very rare or may be extirpated from the Ohio portion of the drainage; the status of these species upstream in the Pennsylvania portion of the watershed was not determined.

Brook stickleback (*Culaea inconstans*) were known from two locales on the escarpment in Conneaut Creek prior to 1954 (Trautman, 1981, p. 537). No tributary streams or wetlands found on the escarpment were supportive of brook sticklebacks during our survey. Brook sticklebacks only occurred at one site within the lake plain, an isolated pond on the Conneaut Creek flood-plain upstream of the SR 20 bridge.

Abundance designations for species found at many sites within the watershed and species richness between sites varied considerably. At least part of the apparent variation was attributed to differences in site habitat structure and available micro-habitats. Some sites contained deeper sections or holes scored in the bedrock, whereas others were shallower and often had swifter water flows.

Seventeen species of fishes listed in Appendix 4 represent drainage system records not listed by Trautman (1981). Many of these species were probably present in the past, but they are either difficult to detect, rare in the watershed, or they are recent introductions. The northern brook lamprey (*Ichthyomyzon fossor*) is an Ohio endangered species (Ohio Department of Natural Resources Division of Wildlife, 2002).

Collection records of native lamprey (12 sites; Appendix 2) indicate occurrences downstream from the Creek Road covered bridge (site 21, river distance 11.7 km) in Conneaut, and 10 of these records occur downstream of the former Grant Street bridge (site 15) or within the first 5.5 river miles. The exotic sea lamprey (*Petromyzon marinus*) occurred at 22 sites throughout the Ohio portion of the drainage system.

Twenty-one species of fishes inhabited only the wide, deeper water sites from near the Center Road bridge (site 13) downstream to the harbor (Appendix 2). The distributions of four species of fishes were restricted to cool, shaded 2nd, 3rd, and large 1st order tributary streams (Appendix 2).

The fathead minnow (*Pimephales promelas*) was one of the rarest species of fishes encountered ($f = 3.4\%$). The normal color morph was only detected at site 14. An orange colored morph referred to as the "rosy red minnow" was found at site 10 in 2000. Three individuals were observed; two of those were collected and preserved. This color variant was first propagated during the early 1980s in Arkansas (Sutton, 1994) for the "feeder" market and then for the bait industry. The rosy red minnows observed in the tributary were probably introduced by sport fisherman or by local aquarists. Survivorship of the rosy red minnow is apparently lower than that of normally colored (wild-type) fatheads (Ludwig, 1996), especially during winter months. Sampling at this site in 2001 did not produce any color variants or wild-type colored fathead minnows.

Rainbow trout (*Oncorhynchus mykiss*) were recorded at only 12 sites. During spawning runs trout pass through all Conneaut Creek main stream sites and many migrate into Pennsylvania. Rainbow trout spawn successfully in a minimum of four Conneaut Creek tributaries. We observed young of the year (age 0) individuals 3–5 cm in total length in streams over multiple years during August with water temperatures reaching 21°C during drought years. The extended presence of predatory young of the year of this introduced species during the stream larval stage of *Desmognathus* and *Eurycea* may cause declines in local stream salamander recruitment through direct predation or through competition for invertebrate food resources. These potential interactions deserve further study.

Invasive round gobies (*Neogobius melanostomus*) were captured ($n = 8$) beneath the Pennsylvania Central Railroad bridge, site 6 (river distance 3.5 km) in mid July of 2002. The OEPA captured one goby at site 2 (river distance 0.2 km) in August 1998. This nuisance species (Office of the Great Lakes, 1996) has apparently expanded its geographic distribution upstream a minimum of 3.3 km since 1998.

Amphibians and reptiles

Three species of reptiles represent new drainage system records (Appendix 4). Five new township records were obtained for four species of amphibians, and 16 new township records were obtained for 11 species of reptiles (Appendix 5).

Jefferson Salamanders (*Ambystoma jeffersonianum*) with three occurrences and the Silvery Salamander (*A. platineum*) with one occurrence are rare species within the Conneaut Creek drainage system. The three sites from which these species were recorded are juxtaposed within the Portage Escarpment on the Blakeslee-Barrows Preserve and Richardson Tract of The Cleveland Museum of Natural History. One of the sites (Figure 1, site 40) was a flood-plain seasonal pool; the second site (41) was an old man-made pond situated above the flood plain on the edge of the upland forest; the third site (42) was an abandoned channel of Conneaut Creek that seasonally contains water. Both salamander species are known from few locales in Ashtabula County (Pfungsten, 1998; Pfingsten and Matson, 2003); the Silvery Salamander is known to be a gynogenetic species and must occur in syntopy with the Jefferson Salamander. We speculate that based upon the extent of our surveys and extensive use of larvae for detecting ambystomatid localities that few additional occurrences of these taxa will be documented in the Ohio portion of Conneaut Creek. An interesting biogeographic similarity exists between the locations of the sites where these taxa occur in Conneaut Creek and where *A. jeffersonianum* occurs in the Ashtabula River drainage (Matson, personal observations). The only known site for the Jefferson Salamander in the Ashtabula River drainage system is on the Portage Escarpment approximately 1.5 km east from where

the river breeches the Ashtabula Moraine and Whittlesey Beach Ridge to flow over the Erie Lake Plain. In the Conneaut Creek drainage system these taxa occur on the Portage Escarpment at sites about 1.1 km east (upstream) of the breach in the Ashtabula Moraine where the creek is deflected to the east over the Erie Lake Plain.

A record of the Northern Red Salamander (*Pseudotriton ruber* (Latreille, 1801)) and one of the Four-toed Salamander (*Hemidactylum scutatum* (Schlegel, 1838)) for Conneaut Incorporated were published by Pfingsten and Downs (1989). It is unclear from the stated locality description if either of these records is from within the Conneaut Creek drainage system or from within a small nearby tributary system draining directly into Lake Erie (R. A. Pfingsten personal communication, 2002). We did not encounter either of these species during our survey of the Conneaut Creek watershed even though considerable search effort was directed toward their detection. Recent records (1991 and 2002) for the Northern Red Salamander on the lake plain at the Kingsville Sand Barrens in Kingsville Township indicate its persistence adjacent to the Conneaut Creek drainage.

The Mudpuppy (*Necturus maculosus*) is now an uncommon and locally rare species in the Ohio portion of Conneaut Creek. But this was not always the case. Prior to the October 1986 application of the lampricide TFM, the Mudpuppy was a common to locally abundant amphibian. Former widespread abundance and stream distribution are based upon salvage collections made during and immediately following lampricide treatment. For example, 56 Mudpuppies were salvaged at the Center Road bridge site (site 67) in 1986. Subsequent searches during this survey and later salvage searches following TFM applications failed to reveal any individuals at this site. We contend that the four additional lampricide applications since 1987 have had a negative impact upon the recovery of this species (Matson, 1998).

Plethodon cinereus, the Red-backed Salamander, occurred at only 14 sites ($f = 18.2\%$). Although apparently suitable upland forested habitat was available (Petranka, 1998), this salamander was usually encountered in small numbers. Annual spring and summer droughts over years probably contributed to its apparent small population sizes and low frequency of detection. The erythristic color morph of this species was found at four sites. One erythristic individual was found at each site, but two of the sites are proximate. This color morph was previously known from only one site in Ashtabula County (Pfingsten and Downs, 1989, p. 232).

Distribution records for Fowler's Toad (*Bufo fowleri*) in northeastern Ohio are confined to Lake and Ashtabula Counties. Six of the existing seven township records in these counties are on the lake plain and most are adjacent to Lake Erie (Walker, 1946; Davis and Menze, 2000; personal observations). All occurrence records for Fowler's Toads in the

vicinity of Conneaut Creek are old records (pre-1946) listed near Farnham and near Conneaut (J. Davis, personal communication, 2003). No Fowler's Toads were detected near Farnham during this survey. However, this species occurred at four sites within the Conneaut Creek gorge. The toads were always either in the channel on sand/gravel bars or along the bank concealed beneath shale slabs. The distribution of this species in Conneaut Creek appears patchy, but additional survey work may fill in gaps and extend the range within the watershed. A similar distribution pattern is developing in the Ashtabula River drainage system. The main difference in the apparent distribution of the Fowler's Toad between the two drainage systems is that Fowler's Toad occurs at the Walnut Beach/Ashtabula Harbor area, whereas the American Toad occupies the Conneaut Harbor area (Matson, unpublished data). Currently, the range of Fowler's Toad in Conneaut Creek extends from site 13 (Center Road) to site 25 (Camp Peet) just north (downstream) of the Arkona Beach Ridge breach.

Three species of reptiles found during the survey were new drainage records (Appendix 4). The Eastern Spiny Softshell Turtle (*Apalone spinifer*) was trapped at three sites ($n = 5$), all on the lake plain. Trapping upstream of Locust Grove Campground (site 29) and downstream of the Conneaut Fish and Game Club (site 18) produced only captures of other turtle species. Additional occurrences both upstream and downstream are probable because suitable habitat exists in both directions. However, the softshell prefers waters with sand or mud bottoms (Ernst and Barbour, 1989, p. 105); the substrate throughout much of the Ohio portion of Conneaut Creek consists of water swept shales. Occurrences are predicted to be local and patchy. The only previously published record for this species in Ashtabula County was in the Grand River (Matson, 1985).

The Stinkpot (*Sternotherus odoratus*) was a rare turtle within the Conneaut Creek drainage system. One specimen, captured in April 2003 at site 82 (Figure 1) during a lampricide application, is a drainage record. We believe the first specimen vouchered from Ashtabula County was collected in Pymatuning Creek in 1997, but this is the first published occurrence record for the county. The specimen from Pymatuning Creek is preserved at the Cleveland Museum of Natural History. A photographic voucher of the Conneaut Creek specimen is also at the Cleveland Museum of Natural History. The Conneaut Creek channel provides few areas with slow current and soft substrate, the preferred habitat of the Stinkpot (Ernst and Barbour, 1989, p. 77). Some deep channel ponds and swamps within the drainage system appear to provide suitable habitat, but trapping results indicate this to be a rare turtle. The proximity of this site to the Ohio-Pennsylvania border coupled with the high water conditions the previous week may have swept the turtle downstream from Pennsylvania waters.

Conant (1951) cited a record of the Spotted Turtle (*Clemmys guttata*) near Farnham in Conneaut Incorporated. We encountered only one individual during our survey. The turtle was located crossing the road at site 76 near large flood-plain channel ponds that supported extensive aquatic vascular plant growth. Repeated trapping of this area over several years and numerous searches failed to detect additional individuals.

Former distribution records of the Queen Snake (*Regina septemvittata*) in the Conneaut Creek drainage system were near Conneaut (Conant, 1951, p. 79). We found new occurrences at sites in Kingsville and Monroe Townships as well as at several sites far upstream in Conneaut, nearly as far as the Ohio-Pennsylvania border. Our recent observations of Queen Snakes were all within the Portage Escarpment from site 47 upstream. Suitable habitat with numerous siltstone slabs was readily available through the Ohio portion of the Conneaut Creek drainage system, and *Orconectes propinquus* (Girard) and *Cambarus robustus* Girard crayfish were abundant food resources.

We have surveyed the fishes, amphibians, and reptiles at numerous sites within the Conneaut Creek drainage system and have attempted to assemble available records from several sources. Fish data from the OEPA and those from The Cleveland Museum of Natural History complemented our field surveys by providing records from wide, deep downstream sites for which we did not have appropriate collection equipment available. Temporal changes in the watershed due to development, landscape alteration, invasive species, and other perturbations will undoubtedly alter the composition and structure of the fish and herpetological communities.

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Appendix 1. Latitudinal and longitudinal coordinates and site names of the locales surveyed or for which species data were available from previous collections. Abbreviations used: dws = downstream; ups = upstream; CMNH = Cleveland Museum of Natural History.

Site Number	Latitude (N)	Longitude (W)	Township	Site Name
1	41° 58' 10.2"	80° 33' 8.8"	Conneaut	Conneaut harbor
2	41° 57' 56"	80° 32' 48"	Conneaut	
3	41° 57' 44"	80° 32' 33"	Conneaut	
4	41° 57' 31"	80° 32' 33"	Conneaut	
5	41° 57' 8.0"	80° 31' 50"	Conneaut	
6	41° 56' 58.5"	80° 32' 49.8"	Conneaut	Penn Central Railroad
7	41° 56' 32.9"	80° 33' 1.4"	Conneaut	Main St. Bridge ups to SR 20
8	41° 56' 30"	80° 32' 57"	Conneaut	North side of SR 20 Bridge
9	41° 56' 23.0"	80° 33' 13.0"	Conneaut	
10	41° 56' 8.0"	80° 33' 42"	Conneaut	
11	41° 56' 13.5"	80° 33' 46.9"	Conneaut	SR 7 Bridge north of Welton Rd.
12	41° 56' 16.0"	80° 33' 51.2"	Conneaut	Mill Rd. Crossing
13	41° 56' 11.5"	80° 34' 18.0"	Conneaut	Center Rd. Bridge ups
14	41° 55' 59.6"	80° 34' 40.6"	Conneaut	
15	41° 56' 0.1"	80° 35' 23.9"	Conneaut	Grant St. Bridge
16	41° 56' 2.6"	80° 35' 42.2"	Conneaut	Conneaut Fish and Game Club beaver dam
17	41° 55' 57.2"	80° 35' 49.8"	Conneaut	Conneaut Fish and Game Club swamp
18	41° 55' 43.3"	80° 35' 33.9"	Conneaut	Conneaut Fish and Game Club CC
19	41° 55' 37.0"	80° 35' 51.5"	Conneaut	Conneaut Fish and Game Club forest
20	41° 55' 37.0"	80° 36' 16.3"	Conneaut	Gaging Station at Keefus Rd.
21	41° 55' 12.0"	80° 36' 36.0"	Conneaut	Creek Rd. Covered Bridge
22	41° 55' 7.0"	80° 36' 45.0"	Conneaut	
23	41° 54' 50.1"	80° 36' 20.7"	Conneaut	Camp Peet
24	41° 54' 32.0"	80° 37' 3.1"	Conneaut	Camp Peet ponds
25	41° 54' 25.8"	80° 37' 1.8"	Conneaut	Camp Peet
26	41° 54' 0.00"	80° 37' 26.3"	Conneaut	Markko Vineyard
27	41° 54' 20.3"	80° 37' 58.3"	Kingsville	
28	41° 54' 30.7"	80° 37' 58.3"	Kingsville	
29	41° 54' 10.7"	80° 38' 46.2"	Kingsville	Locust Grove Campground
30	41° 54' 1.0"	80° 39' 0"	Kingsville	
31	41° 53' 57.4"	80° 39' 11"	Kingsville	
32	41° 54' 0.5"	80° 39' 20"	Kingsville	
33	41° 53' 34.0"	80° 40' 7"	Kingsville	
34	41° 53' 33"	80° 40' 4"	Kingsville	Ridge Rd. Bridge
35	41° 53' 17"	80° 38' 42"	Kingsville	CMNH Blakeslee Barrows Preserve
36	41° 53' 20.2"	80° 39' 48.3"	Kingsville	
37	41° 53' 23"	80° 38' 42"	Kingsville	CMNH Blakeslee Barrows Preserve
38	41° 53' 38.0"	80° 40' 9"	Kingsville	CMNH Blakeslee Barrows Preserve
39	41° 53' 13"	80° 39' 23.5"	Kingsville	CMNH Richardson Tract/Blakeslee Barrows Preserve
40	41° 53' 19"	80° 39' 25"	Kingsville	
41	41° 53' 23"	80° 39' 30"	Kingsville	CMNH Blakeslee Barrows Preserve
42	41° 53' 29"	80° 39' 18"	Kingsville	CMNH Blakeslee Barrows Preserve
43	41° 53' 25"	80° 39' 16"	Kingsville	CMNH Richardson Tract/Blakeslee Barrows Preserve
44	41° 53' 21"	80° 39' 7"	Kingsville	CMNH Richardson Tract/Blakeslee Barrows Preserve
45	41° 53' 35"	80° 38' 30"	Kingsville	CMNH Richardson Tract/Blakeslee Barrows Preserve
46	41° 53' 34"	80° 39' 13"	Kingsville	
47	41° 53' 47.27"	80° 38' 23.5"	Kingsville	
48	41° 53' 31.4"	80° 38' 19.6"	Kingsville	CMNH Hubbard Preserve
49	41° 53' 33"	80° 38' 10"	Kingsville	
50	41° 53' 9.8"	80° 37' 54"	Kingsville	CMNH Hubbard Preserve
51	41° 53' 5.3"	80° 38' 9"	Kingsville	CMNH Hubbard Preserve
52	41° 53' 0.1"	80° 37' 18.2"	Monroe	
53	41° 53' 13.0"	80° 37' 22.4"	Monroe	
54	41° 53' 4.3"	80° 37' 9.9"	Monroe	Hatch Corners Rd. at State Rd.
55	41° 53' 10.1"	80° 37' 4.9"	Monroe	
56	41° 53' 10.0"	80° 37' 15.0"	Monroe	State Rd./Turnpike Rd. Bridge
57	41° 53' 19.7"	80° 36' 45"	Monroe	State Rd. Bridge ups
58	41° 53' 19.0"	80° 36' 28"	Monroe	
59	41° 53' 27.9"	80° 36' 32.1"	Monroe	Horton Rd. Bridge dws
60	41° 53' 50"	80° 36' 3.3"	Conneaut	Southeast of South Ridge at Keefus Rd.
61	41° 53' 14.5"	80° 36' 19.9"	Monroe	
62	41° 53' 11.8"	80° 35' 58"	Monroe	Horton Rd. Bridge area
63	41° 54' 29.0"	80° 35' 36.1"	Conneaut	Underbridge Rd. at Blood Rd.
64	41° 52' 45.9"	80° 35' 29.9"	Monroe	Wetmore Rd. Bridge ups
65	41° 52' 55"	80° 34' 43.2"	Monroe	Hatch Corners roadside ditch
66	41° 53' 31"	80° 34' 58"	Monroe	
67	41° 53' 43.0"	80° 34' 50.8"	Conneaut	Center Rd. Bridge
68	41° 54' 27"	80° 34' 51"	Conneaut	Horton Rd. at powerline
69	41° 53' 39.1"	80° 34' 41.8"	Conneaut	

Site Number	Latitude (N)	Longitude (W)	Township	Site Name
70	41° 53' 39.6"	80° 34' 22.6"	Conneaut	SR 7 and Center Rd. triangle
71	41° 53' 45.3"	80° 34' 23"	Conneaut	Center Rd. Bridge to ups of SR 7 Bridge
72	41° 53' 41.3"	80° 33' 35.9"	Conneaut	Blakesley Rd. terminus
73	41° 53' 34.3"	80° 33' 29.3"	Conneaut	
74	41° 53' 15.2"	80° 32' 30.8"	Conneaut	
75	41° 53' 49.2"	80° 32' 54.2"	Conneaut	
76	41° 54' 7.3"	80° 32' 47.9"	Conneaut	
77	41° 54' 50.3"	80° 33' 16.6"	Conneaut	Middle Rd. Bridge dws
78	41° 54' 4.4"	80° 32' 12.8"	Conneaut	Underridge Rd. at Daton Rd.
79	41° 54' 11.1"	80° 31' 57.5"	Conneaut	
80	41° 54' 12.0"	80° 31' 48.6"	Conneaut	Furnace Rd. Bridge dws
81	41° 54' 20.5"	80° 31' 30.0"	Conneaut	
82	41° 54' 18.7"	80° 31' 13.1"	Conneaut	
83	41° 54' 28.9"	80° 31' 17.1"	Conneaut	Furnace Rd. Bridge ups

Species	Site	72	73	74	75	76	77	78	79	80	81	82	83	Occurrence	f (%)
Polysciidae															
<i>Ichneumonator</i>															
<i>Ichneumonator</i> Reighard and Cummins, 1916 (E)														2	3.4
<i>Ichneumonator unispinis</i> Hubbs and Trautman, 1937														4	6.8
<i>Lamproctes appendix</i> (DeKay, 1842)						A				C				6	10.2
<i>Pteronotus marinus</i> Linnaeus, 1758														22	37.3
Leptosiidae															
<i>Leptosiella oxensis</i> (Linnaeus, 1758)		U				R		U		C				15	25.4
<i>Leptosiella</i>															
<i>Amicallus</i>															
<i>Amicallus</i> Linnaeus, 1766*														2	3.4
Chalcidae															
<i>Aloea pseudoharengus</i> (Wilson, 1811)*														2	3.4
<i>Dorosoma cepedianum</i> (Lesueur, 1818)*														5	8.5
Cynipidae															
<i>Camposoma angustulum</i> (Rafinesque, 1820)		A				A			A			R		28	47.5
<i>Campoplex</i>														3	5.1
<i>Chionostoma elongatum</i> (Kirtland, 1838) ¹														2	3.4
<i>Cyrtidella pilospora</i> (Cope, 1868)						U-C			C					25	42.4
<i>Cyrtus carpio</i> Linnaeus, 1758														5	8.5
<i>Cyrtus carpio</i> x <i>Carissus variatus</i>		A	U			A			R			U-C		2	3.4
<i>Lasius chrysoccephalus</i> Rafinesque, 1820									A					41	69.5
<i>Lasius chrysoccephalus</i> x <i>chrysoccephalus</i>									R					3	5.1
<i>Leptocryptus</i>						C-A			C					6	10.2
<i>Leptocryptus</i> (Grand, 1856)						R			U					12	20.4
<i>Nocantia micropogon</i> (Cope, 1865)														9	15.3
<i>Notamigonus crysolacca</i> (Mitchell, 1814)						C			C-A					22	37.3
<i>Notropis amblyops</i> (Rafinesque, 1820)		C				C								8	13.6
<i>Notropis alternoides</i> Rafinesque, 1818						C								15	25.4
<i>Notropis buccatus</i> (Cope, 1865)									R					1	1.7
<i>Notropis buccatus</i> (Cope, 1865) ²														3	5.1
<i>Notropis photogenis</i> (Cope, 1865)														20	33.9
<i>Notropis rubellus</i> (Agassiz, 1850)		A				C-A			U-C					22	37.3
<i>Notropis stramineus</i> (Cope, 1865)		C				C-A			R					18	30.5
<i>Notropis volucella</i> (Cope, 1865)						U			A			C-A		3	5.1
<i>Phaenocarpa erythrogastra</i> (Rafinesque, 1820) ¹							C							30	50.8
<i>Phaenocarpa notata</i> (Rafinesque, 1820) ¹						A			A					10	16.9
<i>Phaenocarpa notata</i> (Rafinesque, 1820) ²								U						1	1.7
<i>Rhinclitrus aratus</i> (Herman, 1804) ¹														22	37.3
<i>Rhinclitrus cauratus</i> (Valenciennes, 1842)*														6	10.2
<i>Semiothisa atramentaria</i> (Mitchell, 1818)		R	R	A	U	U								33	55.9
Catantopidae															
<i>Carpodacus cyprinus</i> (Lesueur, 1817)						R								6	10.2
<i>Catantopus commersoni</i> (Lacepede, 1803)		A				C			U			R		33	55.9

Species	Site	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Percichthidae																		
<i>Morone chrysops</i> Rafinesque, 1820 ^a																		
<i>Perca flavescens</i> Rafinesque, 1820 ^a																		
<i>Ambloplites rupestris</i> Rafinesque, 1817 ^a												C			A		C	C
<i>Lepomis cyanellus</i> Rafinesque, 1819			C												R		U	R
<i>Lepomis gibbosus</i> (Linnaeus, 1758)															R		R	U-C
<i>Lepomis macrochirus</i> Rafinesque, 1819												U			A		C	U
<i>Micropterus dolomieu</i> Lacepede, 1802			C	C								C						R
<i>Micropterus salmoides</i> (Lacepede, 1802)																		
<i>Perca flavescens</i> Rafinesque, 1820 ^a												R						
<i>Pomoxis nigromaculatus</i> (Lesauze, 1829)												R						R
Percidae																		
<i>Etheostoma blennioides</i> Rafinesque, 1819			A	C											A		C	C
<i>Etheostoma caeruleum</i> Storer, 1845			C	U								U-C			A		C	C
<i>Etheostoma labellum</i> Rafinesque, 1819			C												C		U	C
<i>Etheostoma nigrum</i> (Linnaeus, 1758)			R-U	C								C			C		U	C
<i>Perca flavescens</i> (Mitchill, 1814)																		
<i>Perca caprodes</i> (Rafinesque, 1818)															C			R
<i>Perca maculata</i> (Grand, 1859)			R									R					R	U-C
<i>Stizostedion vitreum</i> (Mitchill, 1818) ^a																		
Schizothoracidae																		
<i>Apollonia genivittata</i> Rafinesque, 1819 ^a																		
<i>Apollonia melanostomus</i> (Pallas, 1814) ^a																		
<i>Notropis melanostomus</i> (Pallas, 1814) ^a																		
Species Richness per Site		0	25	19	1	18	2	0	0	4	0	24	0	1	29	0	29	27

Species	Site	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Percinthyidae																			
<i>Morone chrysops</i> (Rafinesque, 1820) ^a																			
Centrarchidae																			
<i>Lepomis cyanellus</i> Rafinesque, 1817										C		R			R				
<i>Lepomis gibbosus</i> (Linnaeus, 1758)												R			U				
<i>Lepomis microlophus</i> Rafinesque, 1819												U			R				U
<i>Micropterus dolomieu</i> Lacépède, 1802					C					C					C				
<i>Micropterus salmoides</i> (Lacépède, 1802)																			
<i>Pomoxis nigromaculatus</i> Rafinesque, 1818	R																		
<i>Pomoxis nigromaculatus</i> (Lesueur, 1829)												A							
Percidae																			
<i>Etheostoma blennioides</i> Rafinesque, 1819					C					U					C-A				R
<i>Etheostoma caeruleum</i> Stead, 1945	C				C					C					C				C
<i>Etheostoma caeruleum</i> (Linnaeus, 1758)	U													U					C
<i>Etheostoma nigrum</i> Rafinesque, 1820					U					C						U			C
<i>Percis flavescens</i> (Mitchill, 1814)																C			C
<i>Percina caprodes</i> (Rafinesque, 1816)																			
<i>Percina maculata</i> (Grand, 1859)																			
<i>Percina vivax</i> (Mitchill, 1815) ^a	R														R				C
Serranidae																			
<i>Aplodinotus grunniens</i> Rafinesque, 1819 ^a																			
Gobiidae																			
<i>Negobius melanogomus</i> (Pallas, 1814) ^a																			
Species Richness per Site	13	0	3	3	22	0	2	0	0	20	0	9	0	4	24	6	5	0	26

Species	Site	72	73	74	75	76	77	78	79	80	81	82	83	Occurrence	f (%)
Species															
Periclythyidae															
<i>Merone chrysops</i> Rafinesque, 1820 ^a														2	3.4
Centarchidae															
<i>Centarchus varius</i> Rafinesque, 1817 ^b	U-C					U			C-A			U		19	32.2
<i>Leptocentarchus ruficornis</i> Rafinesque, 1819						R			P-U					9	15.3
<i>Leptocentarchus limnaeus</i> (Linnaeus, 1758)						C-A			R			R		15	25.4
<i>Leptomis gibbosus</i> (Linnaeus, 1758)						C			R			R		26	42.5
<i>Leptomis macrochilus</i> Rafinesque, 1819						U			C			R		22	35.8
<i>Micropterus dolomieu</i> Lacépède, 1802	C					R			C			R		10	16.9
<i>Micropterus salmoides</i> (Lacépède, 1802)						R			R			R		4	6.8
<i>Amocetus annularis</i> Rafinesque, 1819														8	13.6
<i>Pseudocentarchus maculatus</i> (Cuvier, 1829)															
Percidae															
<i>Etheostomus bimaculatus</i> Rafinesque, 1819						U			A			U		21	35.6
<i>Etheostomus caeruleum</i> Storer, 1845	C					C			A			U		27	45.0
<i>Etheostomus pholidus</i> Rafinesque, 1819	C					C			C-A			R		20	33.9
<i>Etheostomus nigricans</i> Rafinesque, 1820	C					C			C			C		27	45.0
<i>Etheostomus caeruleum</i> (Storer, 1845)						R			C					7	11.9
<i>Percina caprodes</i> Rafinesque, 1818						R			U-C			R		10	16.9
<i>Percina maculata</i> (Girard, 1859)						R			C					10	16.9
<i>Stizostedion vitreum</i> (Mitchill, 1818) ^a														4	6.8
Sciaenidae															
<i>Aplodinotus grunniens</i> Rafinesque, 1819 ^a														3	5.1
<i>Microstomus minimus</i> Rafinesque, 1819 ^a															
<i>Microstomus melanostomus</i> (Pallas, 1814) ^a															
Species Richness per Site		16	3	0	1	32	3	3	35	3	0	20	0	2	3.4

Appendix 3. Taxa of amphibians and reptiles and an abundance designation for each taxon recorded at each site. See methods section (p. 4–5) for an explanation of designation symbols. Letters in parentheses indicate the status within Ohio as classified by ODNR Division of Wildlife (2002): (E) Endangered, (T) Threatened. Abundance designations followed by a superscript (s) denotes salvaged specimens.

[illegible]

Species	Site	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Ambystomatidae																			
<i>Ambystoma jeffersonianum</i> (Green, 1827)																			
<i>Ambystoma maculatum</i> (Shaw, 1802)																			
<i>Ambystoma plataneum</i> (Cope, 1868)																			
Plethodontidae																			
<i>Desmognathus fusus</i> (Green, 1818)		R	C	R	R					R	U	U			R	U			
<i>Desmognathus ochropleurus</i> Cope, 1859		A		A			C			C	A			A	R			A	
<i>Eurycea blediana</i> (Green, 1818)		U	C									A		U	R				
<i>Plethodon cinereus</i> (Green, 1818)					I		C (6)			C (6)				R (1)					
<i>Plethodon glutinosus</i> (Green, 1818)		C (2)			J		C (5)							C (4)					
Proteidae																			
<i>Desmognathus fusus</i> (Green, 1818)																			
<i>Desmognathus fusus</i> (Green, 1818)																			
Salmandridae																			
<i>Nephelobates viridescens</i> (Rafinesque, 1820)							U	R			R								U
Bufo																			
<i>Bufo americanus</i> Holbrook, 1836																			
<i>Bufo fowleri</i> Hinkley, 1862																			
Hylidae																			
<i>Hyla versicolor</i> LeConte, 1825																			
<i>Pseudacris crepitans</i> (West-Newbold, 1838)																			
Ranidae																			
<i>Rana catesbeiana</i> Shaw, 1802																			
<i>Rana clamitans</i> Latreille, 1801																			
<i>Rana palustris</i> LeConte, 1825																			
<i>Rana pipiens</i> Schaefer, 1792																			
<i>Rana sylvatica</i> LeConte, 1825																			
Cheylidae																			
<i>Chelydra serpentina</i> (Linnaeus, 1758)																			
Knoxiidae																			
<i>Knoxiopsis sylvatica</i> (Latreille, 1801)																			
Tarbiidae																			
<i>Chrysomys pictus</i> (Schneider, 1783)																			
<i>Chrysomys guttatus</i> (Schneider, 1792) (T)																			
Trogonidae																			
<i>Apalone spiniferus</i> (Lacépède, 1827)																			
Crotalidae																			
<i>Dipsosaurus dorsalis</i> (Say, 1823)																			
<i>Lampropeltis triangulum</i> (Lacépède, 1788)																			
<i>Nerodia sipedon</i> (Linnaeus, 1758)																			
<i>Regina septemvittata</i> (Say, 1825)																			
<i>Storeria diademata</i> (Holbrook, 1836)																			
<i>Storeria occipitomaculata</i> (Shore, 1839)																			
<i>Thamnophis sirtalis</i> (Linnaeus, 1758)																			
<i>Thamnophis sirtalis</i> (Linnaeus, 1758)																			
Species richness per Site																			
		7	5	2	11	3	7	4	5	5	2	4	2	5	7	4	3	5	1

Species	Site	72	73	74	75	76	77	78	79	80	81	82	83	Occurrence	f (%)
Amblyostomidae															
<i>Amblystoma jeffersonianum</i> (Green, 1827)														4	5.2
<i>Amblystoma tigrinum</i> (Shaw, 1802)						U				P (L)				19	24.7
<i>Amblystoma platyneurum</i> (Cope, 1866)														1	1.3
Petichodontidae															
<i>Desmognathus fusca</i> (Green, 1818)			C-A		C		C	R					U	26	33.8
<i>Desmognathus otopharyngeus</i> Cope, 1859		U	C-A		C-A	U		C	A			C	A	57	46.1
<i>Eurycea balfouriana</i> (Green, 1818)		R	C		U		A						U	24	31.2
<i>Petichodon cinereus</i> (Green, 1818)							R (L)							14	18.2
<i>Petichodon glutinosus</i> (Green, 1818)		1	C (2)		1	R (L)							1	19	24.7
Proteidae															
<i>Necturus maculosus</i> (Rafinesque, 1818)						U (3) ¹						C (6)		13	16.9
Silurimorphidae															
<i>Notropis viridescens</i> (Rafinesque, 1820)								R						11	14.3
Bolotidae															
<i>Bufo americanus</i> Hobbs, 1836		C	U		C-A		C	C	R			C		35	45.5
<i>Bufo borealis</i> Huxley, 1862														4	5.2
Hylidae															
<i>Hyla versicolor</i> LeConte, 1825						P								5	6.5
<i>Pseudacris crepitans</i> (Ward, Seale, 1838)						C				U		U-C		15	19.5
Ranidae															
<i>Rana caroliniana</i> Shaw, 1802			R			R	R	R	C			U-C		24	31.2
<i>Rana clamitans</i> Latreille, 1801		C	U		C	U	R	A	P (T)					42	54.5
<i>Rana palustris</i> LeConte, 1825		C			C		C-A	A	C					29	37.7
<i>Rana pipiens</i> Schreder, 1782		R				U								10	13
<i>Rana sylvatica</i> LeConte, 1825		R						R						11	14.3
Cheyliidae															
<i>Chelydra serpentina</i> (Linnaeus, 1758)						C (7)								12	15.6
Knoxiidae															
<i>Sternotherus odoratus</i> (Latreille, 1801)												R (1)		1	1.3
Emydidae															
<i>Chrysemys picta</i> (Schneider, 1783)						R (1)		1	1	1				8	10.4
<i>Chrysemys guttata</i> (Schneider, 1792) (T)						R (1)								1	1.3
Trionychidae															
<i>Apalone spiniferus</i> (Lesueur, 1827)														3	3.9
Colubridae															
<i>Diadophis amabilis</i> Linnaeus, 1766														1	1.3
<i>Elaphe obsoleta</i> (Say, 1823)														7	9.1
<i>Lampropeltis triangulum</i> (Lacépède, 1788)												C (3)		5	6.5
<i>Nerodia sipedon</i> (Linnaeus, 1758)						A (7)		C (3)	U (2)	R (1)			2	22	28.6
<i>Regina septemvittata</i> (Say, 1825)						U (2)		1				C (5)		6	7.8
<i>Soreria dorsalis</i> (Hobbs, 1836)						C (3)								5	6.5
<i>Soreria occipitomaculata</i> (Storer, 1839)														1	1.3
<i>Thamnophis amatus</i> (Linnaeus, 1766)														3	3.9
<i>Thamnophis ordinatus</i> (Linnaeus, 1758)						U (2)								11	14.3
Species Reliques per Site															
		8	7	1	6	18	4	11	8	4	1	8	7		

Appendix 4. New drainage system records of fishes, amphibians, and reptiles in the Ohio portion of Conneaut Creek. The source and year of the collection record are listed in column three: United States Fish and Wildlife Service (USFWS), Ohio Environmental Protection Agency (OEPA), and Cleveland Museum of Natural History (CMNH). All CMNH records are represented by a vouchered specimen or photographic voucher (pv).

Scientific name	Common name	Source (year)
<i>Lampetra appendix</i>	American Brook Lamprey	USFWS
<i>Ichthyomyzon fossor</i>	Northern Brook Lamprey	USFWS
<i>Ambloplites caeruleus</i>	Bowfin	OEPA (1998)
<i>Alosa pseudoharengus</i>	Alewife	CMNH (1973)
<i>Dorosoma cepedianum</i>	Gizzard Shad	CMNH (1973)
<i>Osmerus mordax</i>	Rainbow Smelt	CMNH (1973)
<i>Umbra limi</i>	Central Mudminnow	CMNH (1996)
<i>Notemigonus crysoleucas</i>	Golden Shiner	CMNH (1998)
<i>Notropis photogenis</i>	Silver Shiner	OEPA (1999)
<i>Pimephales promelas</i>	Fathead Minnow	CMNH (2000)
<i>Pimephales promelas</i>	Rosy Red Minnow	CMNH (2000)
<i>Moxostoma anisurum</i>	Silver Redhorse	OEPA (1998)
<i>Moxostoma duquesnei</i>	Black Redhorse	OEPA (1998)
<i>Moxostoma macrolepidotum</i>	Shorthead Redhorse	OEPA (8 August-27 Sept. 1989)
<i>Fundulus diaphanus</i>	Eastern Banded Killifish	CMNH (1992)
<i>Morone americana</i>	White Perch	CMNH (1992)
<i>Neogobius melanostomus</i>	Round Goby	OEPA (1998)
<i>Apalone spinifer</i>	Eastern Spiny Softshell	CMNH (1999)
<i>Sternotherus odoratus</i>	Stinkpot	CMNH (2003) (pv)
<i>Elaphe obsoleta</i>	Black Rat Snake	CMNH (2001)

Appendix 5. New Ashtabula County Township records for amphibians and reptiles within the Ohio portion of the Conneaut Creek drainage system. An (*) following the township name indicates that no voucher is available; (pv) indicates that only a photographic slide voucher is available. Townships not designated are represented by a vouchered specimen.

Scientific name	Common name	Township	Date
<i>Bufo americanus</i>	American Toad	Monroe	12 July 1996
<i>Hyla versicolor</i>	Common Gray Treefrog	Kingsville	2 July 1996
		Monroe	10 July 1996
<i>Rana catesbeiana</i>	American Bullfrog	Monroe	21 October 1990
<i>Rana pipiens</i>	Northern Leopard Frog	Kingsville	13 July 2000
<i>Chelydra serpentina</i>	Common Snapping Turtle	Conneaut	25 August 1999
		Monroe	2 August 1999
<i>Sternotherus odoratus</i>	Stinkpot	Conneaut (pv)	13 April 2003
<i>Chrysemys picta</i>	Midland Painted Turtle	Conneaut (pv)	17 August 1999
<i>Apalone spinifer</i>	Eastern Spiny Softshell Turtle	Conneaut	19 August 1999
		Monroe (pv)	28 June 2000
<i>Diadophis punctatus</i>	Ring-necked Snake	Kingsville	25 September 1996
<i>Elaphe obsoleta</i>	Black Rat Snake	Kingsville	15 May 2001
		Conneaut (*)	10 August 1999
<i>Lampropeltis triangulum</i>	Eastern Milksnake	Kingsville	13 June 2000
		Monroe	3 July 2001
<i>Nerodia sipedon</i>	Northern Water Snake	Kingsville	2 July 1996
<i>Regina septemvittata</i>	Queen Snake	Kingsville	27 June 2000
		Monroe (pv)	21 August 2000
<i>Thamnophis sauritus</i>	Ribbon Snake	Kingsville	28 August 2002
<i>Thamnophis sirtalis</i>	Eastern Garter Snake	Conneaut	20 July 1999

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SIMULATED EFFECTS OF NUTRIENT ENRICHMENT BY CANADA GEESE ON MACROPHYTES AND ALGAE IN OHIO LAKES

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ABSTRACT

We tested the hypothesis that phosphorus enrichment in lakes by goose droppings can enhance growth of algae and macrophytes at or above those occurring in nature. Seasonal changes in Canada goose populations were determined on five northeastern Ohio lakes to estimate the amount of nutrients added as goose droppings. Numbers of geese were highest during winter migration, but some resident geese remained year-round. In a laboratory experiment, effects of various goose densities (0 – 2.6×10^3 geese/ha) were simulated by adding different amounts of droppings weekly to 1-L bottles containing lake water, algae and *Ceratophyllum demersum*. After four weeks, dissolved total phosphorus concentrations in bottles receiving 1 dropping/week ($\sim 6000 \mu\text{g P/L}$) was higher than in bottles with other treatments (16 – $75 \mu\text{g P/L}$). Phytoplankton chlorophyll *a* levels and periphyton biomass were highest in the 1 dropping/week treatment. *Ceratophyllum demersum* biomass increased by 4.5 g/plant in the 0.1 dropping/week treatment, but plants senesced in 1 dropping/week treatment. We calculated how much phosphorus was added in goose droppings and how much was taken up by *Ceratophyllum demersum* and periphyton biomass in each treatment, and we estimated that plants took up most of the available phosphorus in 0, 0.0001, and 0.001 droppings/week treatments. However, there was a surplus of phosphorus in 0.01, 0.1, and 1 droppings/week treatments, which simulated 2.6×10^3 , 2.6×10^4 , and 2.6×10^5 geese/ha, respectively. These results indicate that goose droppings can increase macrophyte growth and promote a switch from clear lakes dominated by macrophytes to turbid lakes dominated by algae, but this will probably only occur at goose densities ($26,000$ – $260,000$ geese/ha) that are not likely to occur in lakes in Ohio.

Introduction

Lakes are important sources for drinking water and recreational activities such as swimming, boating, fishing, and waterfowl hunting. Although the need to develop sustainable management strategies for multiple use areas is growing,

achieving this goal can be difficult. For example, contamination by toxins and algal blooms are critical issues in lakes used for drinking water, and high rates of nutrient inputs in many areas make it difficult to maintain macrophyte beds used as refugia for juvenile fish in lakes used for recreation

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(Moss et al., 1980; Brönmark and Weisner, 1992).

Interactions among nutrient levels and growth of algae and macrophytes are complex (Vollenwieder, 1968; Correll, 1998). For example, rooted macrophytes can obtain nutrients from sediments, but phytoplankton and non-rooted macrophytes compete for dissolved nutrients in the water column (Barko and James, 1998). *Ceratophyllum demersum* L. is a common non-rooted macrophyte found throughout temperate regions of the world (Sculthorpe, 1967, p. 167), and absorbs most of its nutrients with foliar uptake (Denny, 1972). This species can reduce phytoplankton abundance with shading (Goulder, 1969) and by the release of allelopathic chemicals (Nakai et al., 1999). However, high turbidity from phytoplankton or resuspension of inorganic sediments from biotic factors (e.g., feeding carp) or abiotic factors (e.g., wave action) will inhibit macrophyte growth and promote dominance by phytoplankton (Spence, 1982; Nagid et al., 2001; Wetzel, 2001, p. 626).

Recently, expanding populations of Canada geese (*Branta canadensis* L.) have become an important management concern in Ohio's lakes. Tens of thousands of Canada geese pass through northern Ohio (Ohio Department of Natural Resources, 2002) as they travel to and from their wintering grounds in the southern United States and breeding grounds in Canada. Since the late 1960s when Canada goose populations were at their lowest levels, populations have steadily increased throughout North America (Ankney, 1996; National Audubon Society, 2002). Historically, most Canada geese only occurred in Ohio during the migratory period (Bookhout et al., 1989). Today however, many geese spend the entire year in Ohio, and these are called "resident" geese.

Waterfowl can contribute substantial amounts of nitrogen and phosphorus to lakes and wetlands with their droppings (Manny et al., 1975; Bazely and Jefferies, 1985; Gere and Andrikovics, 1992; Marion et al., 1994; Manny et al., 1994; Mitchell and Wass, 1995; Moore et al., 1998). Canada geese graze on aquatic and terrestrial vegetation and are often found in urban areas. Geese release an average of 28 droppings per day (Manny et al., 1975), and droppings are a source of nitrogen and phosphorus in lentic habitats (Manny et al., 1994; Moore et al., 1998; Kitchell et al., 1999). Therefore, large populations of Canada geese have the potential to contribute significant amounts of nutrients to lakes (Conover and Chasko, 1985; Ankney, 1996). However, the limnological impact of increasing populations of geese in lakes in Ohio is not clear.

In this study, five lakes in northeast Ohio were surveyed to determine seasonal changes in populations of Canada geese, and goose densities were used to estimate the amount of nutrients hypothetically added by geese to one of these lakes (East Twin Lake). Laboratory experiments were used to test the hypothesis that phosphorus

enrichment by goose droppings could enhance growth of periphyton, phytoplankton, and *Ceratophyllum demersum*, and we examined if this would occur at goose densities occurring in nature.

Methods

Study site description

All surveyed lakes (East and West Twin Lakes, Lake Hodgson, Lake Phippen, and Lake Rockwell) are located in northeastern Ohio (Portage Co.). East and West Twin Lakes are 4 km north of the city of Kent. The watershed of the Twin Lakes is mostly residential, and the shorelines are largely mowed lawns (Cooke et al., 1977). Both lakes are used for recreational purposes, including swimming, fishing, and boating (Cooke et al., 1977). Lakes Hodgson, Phippen, and Rockwell are surrounded by deciduous and coniferous woodland with scattered residential homes. Lake Hodgson is about 5 km east of Kent and is a drinking water reservoir for the city of Ravenna. Lakes Phippen and Rockwell are about 4 km northeast of Kent. Both are drinking water reservoirs for the city of Akron. Morphological and hydrological data of the study lakes are listed in Table 1.

Goose population survey

Seasonal changes in Canada goose numbers on East and West Twin Lakes, Lake Hodgson, Lake Phippen, and Lake Rockwell were determined by counting the number of geese using each lake once every 2–4 weeks from February to October 1999. Surveys were conducted with binoculars at each survey site (20–30 minutes per site) between 12:00 and 17:00. All geese that were swimming on the lake, and grazing, sleeping, or loafing near the edges of the lake were counted. Few geese were observed flying during the survey, and therefore individual geese were probably not counted on more than one lake during a survey.

Nutrient addition experiment

In 2001, a laboratory experiment was used to determine the growth response of *C. demersum* and algae across a wide range of goose densities. East Twin Lake was chosen as the model lake because extensive limnological and ecological work has been conducted there in the past (Cooke et al., 1977; Fleischmann, 1999; Lombardo, 2002). On 17 June 2001, *C. demersum* plants and fresh goose droppings were collected at East Twin Lake. Droppings were stored frozen until used in the experiment. Plants that were approximately 15–20 cm in length were chosen for the experiment, and all macroinvertebrates were removed. Plants were blotted with a paper towel for 10 seconds and their initial wet weight was measured. Wide-mouth Nalgene, bottles (1-L) were filled with filtered (212 µm mesh) East Twin Lake water, and one plant was randomly assigned to each bottle. Periphyton density was sampled by suspending one glass microscope slide

Table 1. Physical characteristics of the five lakes surveyed in 1999.

	East Twin Lake ¹	West Twin Lake ¹	Lake Hodgson ²	Lake Pippin ³	Lake Rockwell ¹
Latitude	41°12'N	41°12'N	41°08'N	41°11'N	41°11'N
Longitude	81°20'W	81°21'W	81°17'W	81°19'W	81°20'W
Watershed area (ha)	334.5 (both Twin Lakes)		376.5	410	53.6/12.8
Altitude above sea level (m)	318	319	330	321	321
Lake surface area (ha)	26.9	34.0	77.5	49.0	250.9
Maximum depth (m)	12.0	11.5	20.7	23.7	9.1
Mean depth (m)	5.0	4.3	7.8	11.9	3.1
Volume (m ³)	13.5 × 10 ³	15.0 × 10 ³	n/a	2.7 × 10 ⁶	7.6 × 10 ⁶
Water renewal time (years)	0.54	1.49	n/a	1.0	0.05

¹ Cooke, 1977² Olive, 1961³ K. Coy, Akron City Water Supply, personal communication

on the side of the container with dental floss. Periphyton were allowed to colonize the slides during a two-week conditioning period. Any macroinvertebrates that were observed in the bottles during this period were removed.

Physical characteristics of some goose droppings were determined. Droppings were thawed and wet weight was measured. Dry weight was measured after drying the droppings at 105° C for 24 hours. Moisture content of droppings was calculated by subtracting dry weight from wet weight. Ash free dry weight (AFDW) was determined after droppings were ignited in a muffle furnace at 550° C for 60 minutes. Organic content was determined by subtracting AFDW from dry weight. Total phosphorus content (TP) of individual droppings was estimated by multiplying dropping dry weight by 1.5 percent as described in Manny et al. (1994).

After the two-week conditioning period, six goose dropping treatments were established: 1) control: no goose droppings added; 2) 0.0001 droppings added/week; 3) 0.001 droppings added/week; 4) 0.01 droppings added/week; 5) 0.1 droppings added/week; and 6) 1 dropping added/week. We calculated the number of droppings (X) that would be deposited daily to East Twin Lake (volume = 13.5 × 10³ L) to get the equivalent concentration for each treatment as:

$$X = [\text{no. of droppings per L}] \times 13.5 \times 10^3 / 7$$

Manny et al. (1975) estimated that one Canada goose releases an average of 28 droppings per day, and we calculated the number of geese (Y) that would produce the number of droppings deposited daily to East Twin Lake for each treatment as:

$$Y = X / 28$$

These calculations show that our treatments simulated the expected amount of droppings added to East Twin by approximately: 0; 69; 690; 69,000; 690,000; and 6,900,000 geese, respectively. Furthermore, given that the surface area

of East Twin Lake is 26.9 ha, our treatments were equivalent to approximately: 0; 26; 2.6 × 10³; 2.6 × 10⁴; and 2.6 × 10⁵ geese/ha (Table 2).

A slurry of goose droppings was made fresh each day it was needed by mixing 10 randomly selecting droppings with 1 L of distilled water. Dilutions of slurry that corresponded to different goose dropping treatments were added once weekly; controls received an equal volume of distilled water each week. Each treatment was replicated five times (30 bottles total), and the experiment ran for four weeks. All bottles were held in an environmental chamber at 15° C with a 14 h light/10 h dark cycle, and light levels were 22–28 microeinsteins/m²/sec at 400–700 nm. Distilled water was added to each bottle every 4–7 days to compensate for losses from evaporation.

At the end of the two-week conditioning period and at the end of the four week experiment, we sampled the water column by slowly pipetting 20 ml of water from each bottle without disturbing any solid debris (e.g. undissolved droppings, senescent plants) in the container. Water column TP was measured using standard methods (Clesceri et al., 1998, p. 6-139). Phosphorus content of solid debris was not measured. At the end of the experiment, periphyton biomass on the microscope slides was measured, and phytoplankton response was determined by measuring chlorophyll *a* concentrations in the water column using standard methods (Clesceri et al., 1998, p. 10-18). Final wet weight of each *C. demersum* was measured after blotting the plant for 10 seconds on a paper towel. Mean change in *C. demersum* biomass was determined by subtracting initial wet weight from final wet weight.

Phosphorus uptake by *C. demersum* and periphyton was estimated to determine whether their growth was limited by the amount of phosphorus available in the different treatments. Available phosphorus was calculated by adding TP measured in the water column at the end of the conditioning period to TP added in droppings over the four week experiment. Periphyton biomass in each container was estimated by calculating the amount of periphyton expected to occur on the

Table 2. Effects of geese at East Twin Lake simulated in the nutrient addition experiment.

Treatment ¹	TP added (μg) ²	Geese	Simulated conditions ³		
			Geese/m ²	Geese/ha	TP/lake (kg)
0	0	0	0	0	0
0.0001	11.04	6.9×10^2	5.2×10^{-4}	26	14.9
0.001	1.104×10^2	6.9×10^3	5.2×10^{-3}	2.6×10^2	1.49×10^2
0.01	1.104×10^3	6.9×10^4	5.2×10^{-2}	2.6×10^3	1.49×10^3
0.1	1.104×10^4	6.9×10^5	5.2×10^{-1}	2.6×10^4	1.49×10^4
1	1.104×10^5	6.9×10^6	5.2	2.6×10^5	1.49×10^5

¹ Number of droppings added per week to 1-L bottles² Amount of TP added as droppings over the four-week experiment³ Number of geese (Geese), number of geese per m² of water (Geese/m²), number of geese per ha (Geese/ha), and TP added over four weeks (TP/lake) at East Twin Lake simulated by each treatment

inside of the 1-L bottle (surface area: 0.055 m²) given the mean periphyton density measured on microscope slides at end of the experiment for each treatment. Published uptake rates (McCormick et al., 2001) for periphyton (1000 μg TP/g periphyton dry weight/day) were used to estimate phosphorus uptake by periphyton over the four week experiment. Lombardo (2002, p. 125-134) reported that uptake rates for *C. demersum* ranged from 1.7–3.2 μg TP/g plant wet weight/day. Because *C. demersum* biomass increased during the four week experiment, expected phosphorus uptake was estimated for initial and final *C. demersum* biomass with both low (1.7 μg TP/g plant wet weight/day) and high (3.2 μg TP/g plant wet weight/day) uptake rates. The range of total phosphorus uptake in the bottles was calculated by adding periphyton uptake to the minimum *C. demersum* uptake (initial biomass; low uptake rate) and the maximum *C. demersum* uptake (final biomass; high uptake rate). We calculated this using the average initial and final biomass over all treatments. We could not estimate phosphorus uptake by phytoplankton because we did not directly measure their biomass, therefore our estimated uptake rates are somewhat conservative.

Statistical analyses

Data were analyzed using SigmaStat Version 2.0 (SPSS Inc. Headquarters, Chicago, Illinois) with an alpha error set at 0.05 for all analyses. Data were first tested for normality and equal variance and were $\log_{10}(x+1)$ transformed when necessary. Data collected at the end of the conditioning period and at the end of the experiment were analyzed separately. Total phosphorus, chlorophyll *a*, *C. demersum* biomass, and periphyton biomass means were compared among goose dropping treatments with one-way ANOVAs followed by Tukey's post-hoc test when significant differences were detected.

Results

Canada goose populations

Goose populations on most lakes were highest during the migration period in February–March and declined to lower

levels during April–October when resident geese remained in the area (Figure 1). Goose populations were an order of magnitude higher during the migration period (mean geese/lake = 136) than during the rest of the year (mean geese/lake = 11). The Twin Lakes and Lake Rockwell had the highest goose populations in February–March (400–500 geese), but numbers in all lakes were < 70 geese in the summer and fall. Physical characteristics and estimated phosphorus content of goose droppings collected at East Twin Lake are presented in Table 3.

Nutrient addition experiment

Initial Total Phosphorus (TP) in the water column was not significantly different among treatments ($P > 0.05$) and ranged from 43–80 μg P/L (Table 4). Final TP was not different among treatments ($F = 90.11$, $P < 0.001$) except that levels in the 1 dropping/week treatment (5984 μg P/L) were significantly higher than all other treatments which ranged from 16–75 μg P/L (Table 4).

Initial *C. demersum* biomass ranged from 3–5 g/plant (Figure 2) and was not significantly different among treatments ($P > 0.05$). *Ceratophyllum demersum* grew well in all treatments, except many plants senesced in the highest treatment (1 dropping/week) by the end of the experiment. There were no significant differences in final *C. demersum* biomass among treatments ($P > 0.05$). However, there was a general pattern that biomass increased slightly from 0 to 0.1 droppings/week treatments and then sharply declined at 1 dropping/week, as plants died off (Figure 2). Change of *C. demersum* biomass was different among treatments ($F = 5.885$, $P < 0.002$). During the four week experiment, biomass of *C. demersum* decreased 1.4 g/plant in the 1 dropping/week treatment, which was different than in the 0.1 dropping/week treatment where biomass increased 4.5 g/plant. Changes in *C. demersum* biomass were not significantly different among any other treatments.

Periphyton biomass was higher in the 1 dropping/week treatment than all other treatments ($F = 4.898$, $P < 0.005$)

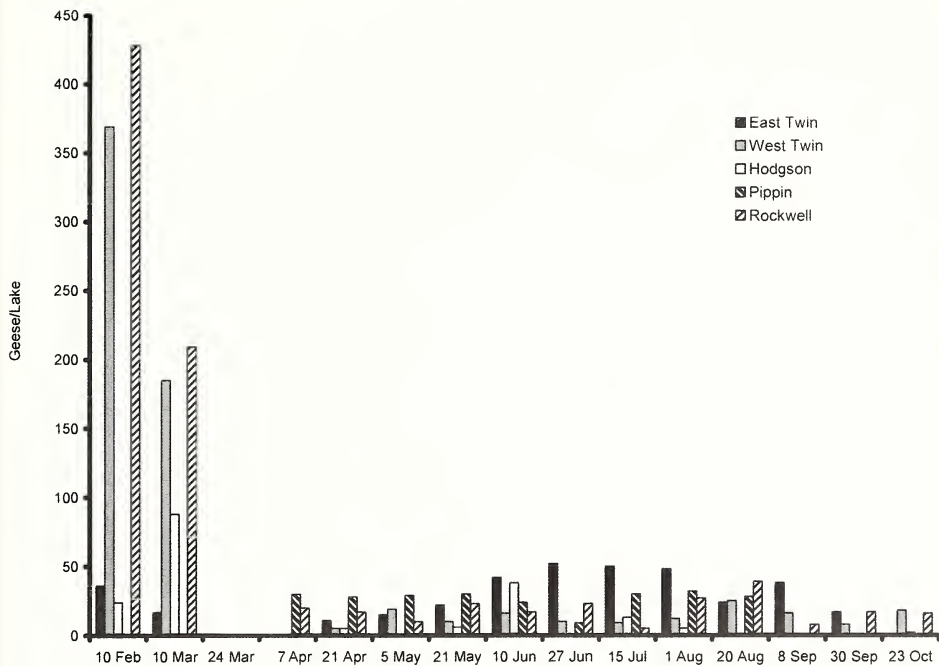


Figure 1. Canada goose populations on five northeast Ohio lakes in 1999.

(Figure 2), and chlorophyll *a* levels were higher in the 1 dropping/week treatment than the 0.0001 dropping/week treatment ($F = 11.716$, $P < 0.001$) (Figure 2). The water in the control treatment bottles was almost clear. Water in the 1 dropping/week treatment bottles was turbid with a dark yellowish-brown color, and the surface was covered with debris from droppings and dead *C. demersum*. Water in the 0–0.1 dropping/week treatment bottles was light yellow with almost no floating debris.

Table 5 reports the amount of phosphorus that we estimated was available in the bottles, and the amount of phosphorus taken up by *C. demersum* plants and periphyton in each treatment. Estimated total phosphorus uptake by periphyton and *C. demersum* was above available TP in the 0, 0.0001, and 0.001 droppings/week treatments, but there was a surplus of TP in the 0.01, 0.1, and 1 droppings/week treatments.

Discussion

This research demonstrates that geese can affect periphyton, phytoplankton, and macrophytes in lakes through the

addition of nutrients in their droppings. *Ceratophyllum demersum* and algae grew slowly in control treatments that had little available phosphorus. There was an insignificant trend of higher growth with increasing phosphorus added in droppings. The highest *C. demersum* and algae growth were found in the 0.01 and 1 dropping/week treatments, respectively. These treatments also had the most surplus phosphorus. Much of the phosphorus not taken up by plant growth remained in the bottles as debris from undissolved droppings, especially in the 1 dropping/week treatment bottles. Therefore, additional phosphorus would become available if this material decomposed. These data suggest that growth of *C. demersum* and periphyton at the 0–0.001 droppings/week treatments were limited by available phosphorus levels, but more phosphorus was added at higher treatment levels than could be taken up by *C. demersum* and algae.

Shallow lakes tend to be either turbid with abundant phytoplankton or clear with abundant macrophytes (Scheffer et al., 1993). Habitats that are extremely eutrophic ($> 1000 \mu\text{g P/L}$) such as wastewater treatment plants are generally dominated by

Table 3. Mean (\pm one standard error) physical characteristics of one goose dropping.

	N ¹	Mean \pm SE
Wet weight (g)	72	11.9 \pm 0.9
Dry weight (g)	72	1.8 \pm 0.1
Ash free dry weight (g)	24	1.07 \pm 0.1
Percent moisture content	72	84.5 \pm 1.8
Organic content (g)	24	0.70 \pm 0.08
P content (g) ²	72	0.0276 \pm 0.002

¹ Indicates the number of droppings used to determine the measurement² Estimated from data presented in Manny et al. (1994)**Table 4.** Mean (\pm one standard error) total phosphorus (TP) concentrations (μ g P/L) measured in the water column of 1-L bottles of nutrient addition experiment. Each treatment was replicated five times.

Treatment ¹	Initial TP ² Mean \pm SE (N=5)	Final TP ³ Mean \pm SE (N=5)
0	47.21 \pm 6.52	16.11 \pm 1.78 a
0.0001	56.50 \pm 7.40	42.11 \pm 9.35 a
0.001	70.43 \pm 15.01	34.51 \pm 9.26 a
0.01	43.34 \pm 5.39	38.83 \pm 8.30 a
0.1	50.31 \pm 4.24	74.78 \pm 12.38 a
1	79.72 \pm 12.75	5983.90 \pm 295.85 b

¹ Treatments are the number of droppings added per week.² TP at the end of the conditioning period³ TP at the end of the experiment. Values with different letters are significantly different.

phytoplankton comprised mostly of cyanobacteria (Jeppesen et al., 1994). Because phytoplankton get their nutrients from the water column, algal biomass is low under low nutrient conditions (Moeller et al., 1988). Therefore, oligotrophic lakes with low nutrient levels ($< 10 \mu\text{g P/L}$) are usually dominated by macrophytes that obtain nutrients from sediments (Scheffer et al., 1993). Lakes can exist in either state at intermediate nutrient levels (Balls et al., 1989; Beklioglu and Moss, 1996), but Irvine et al. (1989) suggested that once phytoplankton are dominant, macrophytes can be permanently suppressed due to light attenuation. In the nutrient addition experiment, algae were most abundant at concentrations of $\sim 6000 \mu\text{g P/L}$ (i.e., the final TP in 1 dropping/week treatment), but the highest growth of *C. demersum* occurred at $75 \mu\text{g P/L}$ (i.e., the final TP in 0.1 dropping/week treatment). Therefore, the switch from a macrophyte to an algae dominated system occurred between the 0.1 and the 1.0 dropping/week treatments, which corresponds to densities of 26,000–260,000 geese/ha.

Several factors may have caused the dramatic decline of *C. demersum* at the 1 dropping/week treatment. For example, decreased light on *C. demersum* leaves caused by phytoplankton or periphyton and elevated concentrations of toxic

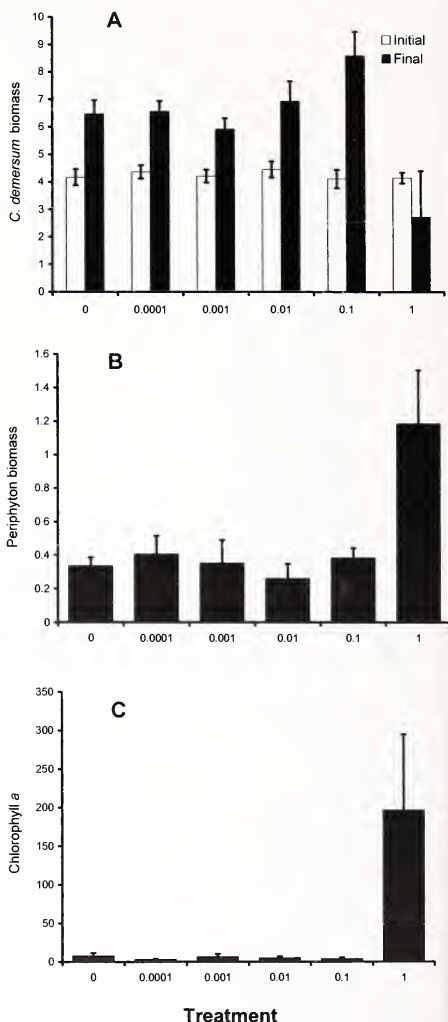
**Figure 2.** Amounts of *C. demersum*, periphyton, and chlorophyll *a* in the nutrient addition experiment. Treatment indicates the number of droppings added per week. A, mean (\pm one standard error) wet weight (g) of *C. demersum* at end of conditioning period (initial) and at end of experiment (final). B, final mean (\pm one standard error) periphyton biomass (g/m^2) collected on microscope slides. C, final mean (\pm one standard error) chlorophyll *a* concentration ($\mu\text{g Chl a/L}$) in the water column.

Table 5. Estimated phosphorus (μg) available and taken up by *C. demersum* and periphyton in the four-week nutrient addition experiment.

Treatment ¹	TP available ²	Initial		<i>C. demersum</i> ³		Periphyton ⁴	Total uptake ⁵	
		low	high	low	high		minimum	maximum
0	47.21	198.40	373.45	307.71	579.23	18.47	216.87	597.70
0.0001	67.54	207.54	390.66	312.29	587.84	22.28	229.82	610.12
0.001	180.00	200.40	377.22	281.68	530.22	19.35	219.75	549.57
0.01	1147.00	212.01	399.08	330.03	621.23	14.37	226.38	635.59
0.1	11,090.00	195.45	367.90	408.77	769.44	21.11	216.56	790.55
1	110,480.00	197.35	371.48	129.73	244.19	65.09	262.44	309.29

¹ Number of droppings added per week² Total available dissolved phosphorus ($\mu\text{g/L}$) = mean TP in water column + TP in droppings added to 5 replicates of each treatment during the 4 week experiment³ *C. demersum* uptake estimated using initial and final mean plant biomass and low (1.7 μg TP/g plant wet weight/day) and high (3.2 μg TP/g plant wet weight/day) uptake rates reported by Lombardo (2002, p. 125)⁴ Periphyton uptake rates (1000 μg TP/g periphyton dry weight/day) reported in McCormick et al. (2001)⁵ Combined uptake by *C. demersum* and periphyton. Minimum uptake estimated for initial *C. demersum* biomass and the low uptake rate. Maximum uptake estimated for final *C. demersum* biomass and the high uptake rate.

compounds from blue-green algae or decomposition of droppings could have negatively affected *C. demersum* plants. Another potential mechanism is that floating and deposited debris from droppings directly shaded the *C. demersum* plants. Shading by inorganic sediments has been shown to decrease growth of submerged macrophytes and increase algal growth (Hough et al., 1989). Moreover, high numbers of waterfowl can remove a large percent of vegetation in lakes and wetlands (Giroux and Bedard, 1987; Woolhead, 1994), which would otherwise shade out phytoplankton in the water column. Further research could examine if goose grazing, in conjunction with the addition of nutrients and debris in their droppings, can act as a suite of co-occurring factors that promote conditions leading to turbid algae-dominated lakes.

Management implications

Numbers of geese observed at the five lakes we surveyed (Figure 1) were below those we have shown to promote algal blooms or suppress macrophyte growth. For example, peak numbers of migratory geese observed at East and West Twin Lakes would have hypothetically added only ~400 g P/day. If all of their droppings were deposited in East Twin Lake, it would raise phosphorus concentrations in the lake by only 2.3×10^{-6} μg P/L. East Twin Lake water column concentrations measured in this study were 43–79 μg P/L, and concentrations reported by Cooke et al. (1977) were 76–94 μg P/L. Therefore, inputs from peak numbers of geese observed on these lakes would have negligible effects on lake nutrient levels. Numbers of geese were slightly higher at Lake Rockwell. However, this lake is much larger than the Twin Lakes, and therefore, expected impacts of the additional nutrients would be minimal.

Our experiments demonstrate that low to moderate goose populations probably do not add enough nutrients to promote a switch from macrophyte to algal dominance in lakes

we surveyed. Although the highest treatment (1 dropping/week) caused a sharp increase in phytoplankton, goose densities (260,000 geese/ha) simulated by this treatment are unlikely to occur in Ohio. For example, peak numbers of geese observed in northern Ohio in 2001 were only 55,000 geese (Ohio Department of Natural Resources, 2002). Furthermore, the number of geese corresponding to 260,000 geese/ha could not physically fit on the surface of a lake at one time. Therefore, the goose densities simulated at the 0.1 and 1.0 droppings/week treatment are not likely to occur in lakes in Ohio. However, it is important to note that others (e.g., Kitchell et al., 1999) have reported that nutrient additions from high numbers of waterfowl can cause algal blooms in some natural aquatic habitats. The effects of nutrient addition by geese will interact with other abiotic and biotic factors such as nutrient enrichment from other sources, biotic stresses, or co-occurring changes in pH, temperature, or light levels. For example, lakes where herbivores reduce macrophyte beds may have algal blooms at lower nutrient addition levels than lakes with abundant macrophytes. Furthermore, inputs of goose droppings to lakes may not be constant over time or within a lake. For example, if 690 geese overwintered for three months on a frozen area within East Twin Lake, about 45 kg of phosphorus could accumulate from goose droppings. This amount of phosphorus may have a local impact on algae and plants after ice melt in spring.

More research is needed to fully understand how nutrients from geese affect macrophytes and algae in lakes. Microcosm experiments, like our nutrient addition experiment, do not always predict biotic responses in natural habitats because there may be scale-dependent effects of treatments (Petersen et al., 1999), and because scientists cannot test for interactions among all potential variables (Cooper and Barmuta, 1993). For example, other factors have been shown to affect whether lakes switch between macrophyte

and phytoplankton dominated equilibria including: 1) invertebrate herbivory of epiphytes and phytoplankton (Timms and Moss, 1984; Brönmark and Weisner, 1992); 2) fish predation of herbivorous zooplankton (Grimm, 1989); 3) macrophyte production of allelopathic chemicals that suppress phytoplankton (Wium-Anderson et al., 1987); and 4) turbidity caused by wave action (Schiemer and Prosser, 1976; Nagid et al., 2001). However, the design of our nutrient addition experiment eliminated all of these variables, and treatment effects may have been different under other conditions (e.g., in macrophyte beds with high species diversity or at different macrophyte densities). Moreover, our experiment only tested the response of plants and algae over a relatively short period (i.e., 4 weeks). Long-term impacts of nutrient addition may be different. Future research should examine interactions of nutrient addition by geese, algal grazers, predatory fish, and wind action under natural conditions.

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THE SNAIL-KILLING FLIES OF OHIO (INSECTA: DIPTERA: SCIOMYZIDAE)

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ABSTRACT

The snail-killing flies (Insecta: Diptera: Sciomyzidae) are a moderately speciose family of true flies with more than 200 species in North America. The biology of all species appears tied intimately to freshwater and terrestrial Mollusca, including snails, snail egg masses, slugs, and fingernail clams. Keys are presented to adults of 99 species of snail-killing flies that occur in Ohio and bordering states. Locality records, habitat, seasonal distribution, larval feeding habits, and references to descriptions of immature stages are given for the 72 species known to occur in Ohio.

Introduction

The family Sciomyzidae, commonly known as snail-killing flies or marsh flies, is worldwide in distribution, with over 500 described species (Rozkošný, 1995). There are nearly 200 species in North America (Knutson et al., 1986), and 72 species have now been recorded from Ohio. The larvae of most species in Ohio are known to attack a variety of prey belonging to aquatic, shoreline, and terrestrial species of snails and slugs. Interesting adaptive divergences from the habit of consuming snails include the genus *Renocera* which has larvae that attack fingernail clams (Foote, 1976, p. 123). Young larvae of *Antichaeta* feed within the egg masses of pulmonate snails, whereas older larvae attack larger, hatched snails (Knutson, 1966).

In this paper, we summarize the distribution, larval feeding habits, and life histories of the 72 species actually recorded from Ohio. Keys are presented for these plus an additional 27 species that have been recorded in states bordering Ohio.

Collecting Sciomyzidae

Most species of Sciomyzidae are associated with wetlands, riparian areas, vegetated road-side ditches, and pond and lake margins, but a number of more terrestrial species are found exclusively in moist areas of herbaceous understory in forests. Many specimens were obtained using an aerial sweep net. Swinging a net briskly and keeping the opening fully within herbaceous vegetation will obtain

specimens taking refuge within plant stands. When a particular stand of vegetation is swept and is identifiable (e.g., sweeping a cattail stand), specimens should be collected in separate vials for each vegetation type and these data included on specimen labels.

Trapping will also procure many specimens, and may obtain species only rarely taken with sweep netting. Pan traps and malaise traps should be positioned near or within vegetation where preliminary sweep netting indicates that adults are active, or in areas where freshwater mollusks are found. Sticky traps may also be employed, but unless a proper solvent is used, adhesives remain and obscure specimens.

Adult Sciomyzidae are killed effectively with killing jars or freezing. Freezing is often preferred because they can be thawed, pinned, and the male postabdomen easily removed before the specimens become dry and brittle. Adult specimens can be placed directly in ethanol for storage and removal of male postabdomens. However, critical point drying or chemical drying (e.g., use of hexamethyldisilazane or other drying agent) is necessary to produce pinnable or pointable material. For those specimens requiring genitalic examination, it is often desirable to simply remove half of the abdomen with iris scissors or ultra-fine forceps. Removing the male postabdomen from completely dry specimens (as in older pinned material) should be done carefully to prevent damage of the genitalic structures and the body anterior of the abdomen.

Rearings have provided invaluable information on the trophic adaptive radiation that has occurred in the Sciomyzidae (Berg and Knutson, 1978; Foote, 1996a). All North American species are restricted to feeding on Mollusca, including snails, snail egg masses, slugs, and fingernail clams. Keeping infested molluscs in the laboratory may produce new host association data when adults emerge from puparia. Species that pupariate away from their hosts can be collected from leaf litter, or can be found next to emergent objects in standing water. Puparia should be placed in rearing jars with a moist substrate, such as peat moss. Rearing species from egg to adult should be done following the methods of Foote (1996a, p. 4).

Identification of Sciomyzidae

Terminology used in this paper follows that of Knutson (1987). The keys rely heavily on external adult characters for identification, including unique color patterns of the body, wing patterns, position of setae (i.e., chaetotaxy), and morphology of specific body parts such as antennae. However, examination of the male postabdomen is frequently necessary to identify specimens to species, or to confirm determinations based on external morphology. This is especially true of the genera *Dictya* and *Limnia*, many *Pherbellia*, and some *Tetanocera*.

Genitalia must be cleared with potassium hydroxide (KOH) for proper examination of diagnostic characters. Genitalia were removed from males with microdissection forceps or scissors, placed into 10 percent KOH, and either left overnight or gently heated for 20–30 minutes. A few drops of glacial acetic acid was added to specimens once cleared, neutralizing the KOH and preventing further maceration of the tissues during permanent storage. Genitalia were placed in 70 percent ethanol for examination, then in genitalia vials (rubber or plastic caps are preferred to cork) containing liquid glycerol for permanent storage. The genitalia vial caps were pierced with the specimen pin below the adult and positioned above all data labels.

The most important, and obvious, character used during genitalic examination is the surstylus (Figure 11F). This is a triangular or rectangular structure that can be exposed by unfolding the genitalia. In some species it should be viewed from both lateral and posterior perspectives. In other cases, viewing the gonite, hypandrium, or the aedeagus is necessary. The cerci and epandrium (Figure 11F) are of little or no diagnostic use during genitalic examination. The examination is done with the point of fine forceps or a dissecting needle placed near the sixth sternite and pulling the genitalic structures out to expose them. This method also exposes the gonite (Figure 10E) and hypandrium (Figure 10E) when necessary. Most of the useful details of the hypandrium are found on the ventral process, which may be triangular, rectangular, or multi-lobed (Figure 11A). The aedeagus is membranous protrusion exposed when the genitalia are unfolded, and is occasionally useful for species identification.

Material Examined

The data for most specimens presented in this work were maintained on a database by the senior author since the 1960s. Many are currently housed at The Cleveland Museum of Natural History (CMNH), the Carnegie Museum of Natural History (CMNH), the Illinois Natural History Survey (ILNHS), Iowa State University (IASU), Florida State Collection of Arthropods (FSCA), the University of Minnesota (UMN), the United States National Museum (USNM), or the Ohio State University (OSU). Others reside in the personal collection of the senior author (BAF), which will eventually be deposited in The Cleveland Museum of Natural History. We summarized North American distributional data for many species from the catalog of Knutson et al. (1986), unless otherwise cited.

Key to Species Occurring in Northeastern North America

Keys are given to 99 species that occur in Ohio and neighboring states (Indiana, Kentucky, Michigan, Pennsylvania, and West Virginia). The 72 species occurring in Ohio are indicated by an asterisk (*).

Key to Genera of Sciomyzidae

1. Proepisternal bristle well developed (Figure 1A); or, proepisternal bristle hairlike and first tarsomere white, strongly contrasting other tarsomeres (*Atrichomelina*) SCIOMYZINI 2
- 1'. Proepisternal bristle absent; all tarsomeres dark or subdued TETANOCERINI 7
- 2(1). Proepisternal bristle hairlike; first tarsomere white and remaining tarsomeres dark; gray fly approximately 6 mm long; widespread and common *Atrichomelina*
1 species, *A. pubera* (Loew)*
- 2'. Proepisternal bristle thick, well-developed; all tarsomeres dark or subdued; size and color variable 3
- 3(2'). Fore tibia with one preapical dorsal bristle 4
- 3'. Fore tibia with two preapical dorsal bristles 6
- 4(3). Anal vein (A1) not reaching posterior margin of wing; frons dull black; uncommon, not recorded from Ohio *Colobaea*
1 species, *C. americana* Steyskal
- 4'. Anal vein (A1) reaching posterior margin of wing or nearly so (Figure 1A); frons dull yellow or shiny, but never black 5
- 5(4'). Frons shiny; fore femur usually with a series of closely spaced, small spinules (pecten) anteromedially that appear as a short dark comblike structure (Figure 1B, Figure 2A); thorax dark and shiny; uncommon *Pteromicra*
- 5'. Frons dull; fore femur lacking pecten; thorax dull yellow, brown, or gray; variable sized flies (Figure 2B-C); common *Pherbellia*
- 6(3'). Arista black (Figure 1E); two orbital bristles present; presutural intra-alar bristle present; two postsutural dorsocentral bristles present. Face in profile sharply concave; grayish flies, somewhat uncommon *Sciomyza*
- 6'. Arista white (Figure 1F); one orbital bristle present; presutural intra-alar bristle absent; one postsutural dorsocentral bristle present; face in profile concave, but with upper area bulging somewhat; uncommon *Oidenatops*
1 species, *O. ferrugineus* Cresson*
- 7(1'). Ocellar bristles present (Figure 1G); crossvein dm-cu straight or nearly so 8
- 7'. Ocellar bristles usually absent; crossvein dm-cu strongly curved 18
- 8(7). Body yellowish, heavily spotted (Figure 2D); wing with heavy pattern (Figure 4A); face convex;

uncommon *Poecilographa*1 species, *P. decora* (Loew)*

- 8'. Body lacking heavy spotting; other characters variable 9
- 9(8'). Subalar sclerite without valar bristles (Figure 1A) 10
- 9'. Subalar sclerite with valar bristles 16
- 10(9). Hind tibia with two preapical dorsal bristles (Figure 1C); only katepisternum with bristles, arista white; uncommon *Antichaeta*
- 10'. Hind tibia with one preapical dorsal bristle; setation on thoracic pleura various; arista white or black ... 11
- 11(10'). Second antennal segment less than one-third length of first flagellomere; arista black; wing not patterned (Figure 2E) *Renocera*
- 11'. Second antennal segment at least one-half length of first flagellomere (Figure 1F); arista black or white; wing patterned or not 12
- 12(11'). Anepisternum and anepimeron with bristles; one orbital bristle or three dorsoventral bristles present 13
- 12'. Anepisternum and anepimeron bare or with hairs; two orbital and two dorsocentral bristles present 14
- 13(12). Face white, without central black spot; two orbital bristles present; three dorsocentral bristles present; all thoracic pleurites bristled; wing heavily and darkly patterned; uncommon, not recorded from Ohio *Hoplodictya*
1 species, *H. acuticornis* (Wulp)
- 13'. Face white, with central black spot (Figure 1G); one orbital bristle present; two dorsocentral bristles present; katepisternum with hairs but without bristles; wing heavily and darkly patterned (Figures 2F, 4B); common *Dictya*
- 14(12'). Arista black; wing hyaline, clouded (Figure 5C), or sometimes spotted (Figure 5D-E); body generally brownish or yellowish (Figure 3A); common *Tetanocera*
- 14'. Arista white; wing densely patterned with dark network around hyaline spots 15
- 15(14'). Face flat to slightly concave; pedicel less than twice as long as wide, compressed; wing relatively broad, dark with numerous hyaline spots (Figure 4C); locally abundant *Euthycera*
1 species, *E. arcnata* (Loew)*
- 15'. Face tuberculate; pedicel twice as long as wide (as in Figure 1E), cylindrical; wing not notably broad;

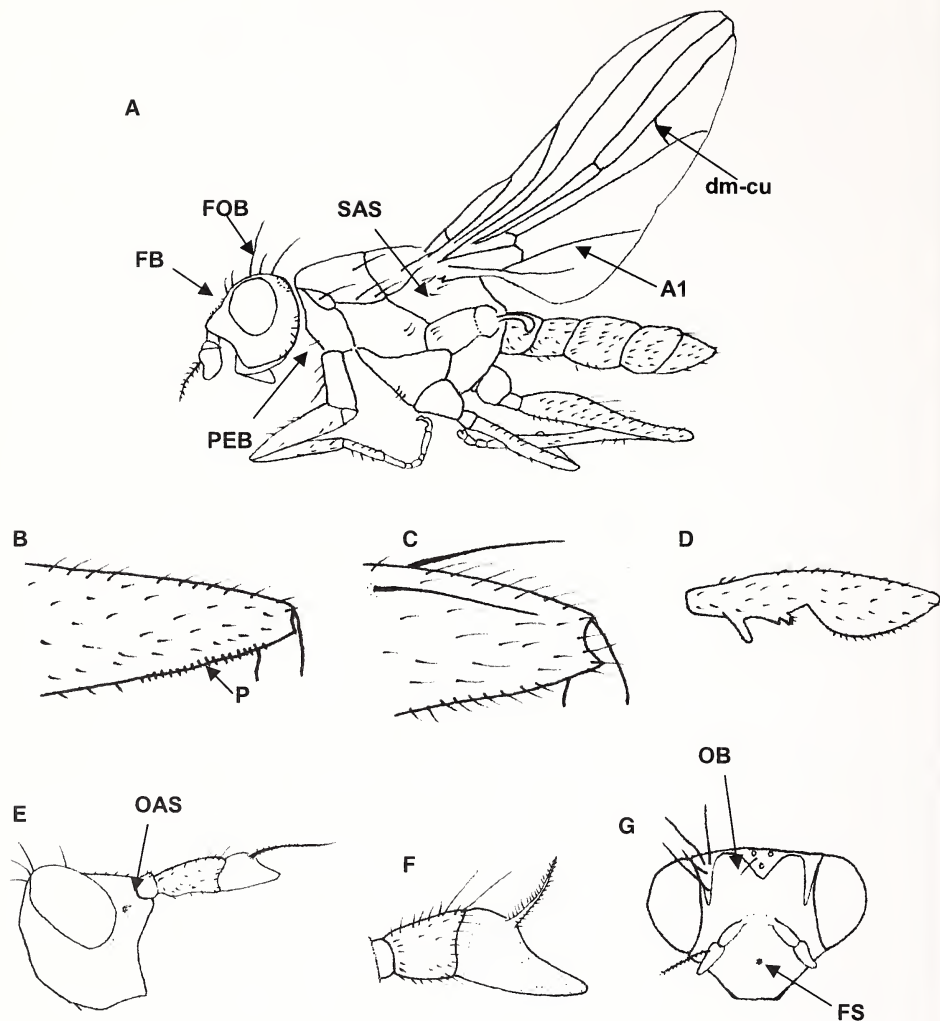


Figure 1. A, hypothetical Sciomyzidae adult, lateral view. A1 = anal vein; dm-cu = posterior cross vein; FB = frontal bristle; FOB = fronto-orbital bristle; PEB = proepisternal bristle; SAS = subalar sclerite. B, left femur of *Pteromicra* sp. P = pecten. C, left femur of *Tetanocera* sp. D, left femur of *Sepedon armipes*. E, head of hypothetical Sciomyzidae, lateral view. OAS = orbitoantennal spot. F, antenna of hypothetical Sciomyzidae, lateral view. G, head of hypothetical Sciomyzidae, anterior view. FS = facial spot; OB = ocellar bristle.

- uncommon *Dictyacum*
- 16(9'). Prescutellar acrostichal bristles absent; mid tibia without distinct preapical dorsal bristle; prosternum bare; arista black; uncommon, not yet recorded from Ohio *Pherbectia*
1 species, *P. limentitis* Steyskal
- 16'. Prescutellar acrostichal bristles present; mid tibia with at least one distinct preapical dorsal bristle; other characters variable 17
- 17(16'). Arista white; frontal vitta broad, shiny; anepisternum and anepimeron haired but without bristles; wing with heavy pattern (Figures 3B, 6A—E); common *Limnia*
- 17'. Arista black; frontal vitta narrow, waxy; anepisternum and anepimeron haired and with bristles; wing patterned as in Figure 4D; uncommon *Trypetoptera*
1 species, *T. canadensis* (Macquart)*
- 18(7'). Ocellar bristles present, well-developed; two pairs of scutellar bristles present; hind coxa with hairs posteromedially; crossvein dm-cu strongly bent (Figure 4E); body yellowish; common *Elgiva*
- 18'. Ocellar bristles absent, or occasionally hairlike; one or two pairs of scutellar bristles; hind coxa usually without hairs posteromedially; crossvein dm-cu straight to bent 19
- 19(18'). Two orbital bristles present, anterior one smaller; postpronotal bristle present; crossvein dm-cu S-shaped; uncommon, not recorded from Ohio *Hedria*
1 species, *H. mixta* Steyskal
- 19'. One orbital bristle present; postpronotal bristle absent; crossvein dm-cu straight to slightly curved; body reddish orange to reddish brown, often with elongate antennae (Figures 1E, 3C); common *Sepedon*

Key to Species of *Pteromicra* Lioy

1. Fore femur black, lacking pecten; anepimeron with two or three long bristles; two pairs of fronto-orbital bristles; antenna entirely black *P. anopla* Steyskal
- 1'. Fore femur color variable, with pecten; anepimeron with small patch of short hairs only; other characters variable 2
- 2(1'). Palpi entirely black 3
- 2'. Palpi entirely yellow, or yellow with black apically 5
- 3(2). Two pairs of fronto-orbital bristles, anterior pair much shorter; dorsum of thorax mostly yellowish, blackish only anteriorly *P. steyskali* Foote
- 3'. One pair of fronto-orbital bristles; other characters variable 4

- 4(3'). Thoracic pleura entirely dark brown or black; meron and katepisternum with dense white pubescence; head mostly black *P. plenralis* (Cresson)*
- 4'. Thoracic pleura mostly yellowish or light brown; meron yellow; meron and katepisternum with sparse, whitish pubescens *P. pectorosa* (Hendel)
- 5(2'). One pair of fronto-orbital bristles; arista brown, long plumose; first flagellomere usually darkened apicodorsally *P. sphenura* Steyskal*
- 5'. Two pairs of fronto-orbital bristles; other characters variable 6
- 6(5'). Metapleuron (area surrounding posterior spiracle) black; hind legs entirely yellow *P. albicaecata* (Cresson)
- 6'. Metapleuron (area surrounding posterior spiracle) mostly yellowish; apex of hind femur blackish *P. similis* Steyskal*

Key to Species of *Pherbellia* Robineau-Desvoidy

1. Wing with distinct pattern 2
- 1'. Wing lacking distinct pattern 4
- 2(1). Wing with dark bands or spots (Figures 2C, 5A-B) 3
- 2'. Wing lacking bands, cell r_1 darkened apically *P. albovarva* (Coquillett)*
- 3(2). Wing with costal margin darkened, distinct banding in cell r_{2+3} (Figure 2C); common *P. nana nana* (Fallén)*
- 3'. Wing with costal margin spotted, and spots throughout wing membrane (Figure 5B) *P. schoenherri maculata* (Cresson)*
- 4(2'). Interfrontal stripe extending at least half way from anterior ocellus to anterior margin of frons 5
- 4'. Interfrontal stripe extending half distance or less from anterior margin of frons 9
- 5(4). Only one pair of fronto-orbital bristles; body grayish red; male genitalia as in Figure 7A *P. parallela* (Walker)*
- 5'. Two pairs of fronto-orbital bristles 6
- 6(5'). Arista almost bare; fronto-orbital bristles strong and nearly equal *P. tenuipes* (Loew)
- 6'. Arista pubescent, with short, fine, closely set hairs; anterior fronto-orbital bristle usually much smaller than posterior bristle 7
- 7(6'). Crossveins of wing clouded; frontal vitta extending narrowly to frontal margin; surstylus narrow apically (Figure 7B) *P. beatricis* Steyskal*
- 7'. Crossveins of wing not clouded; other characters

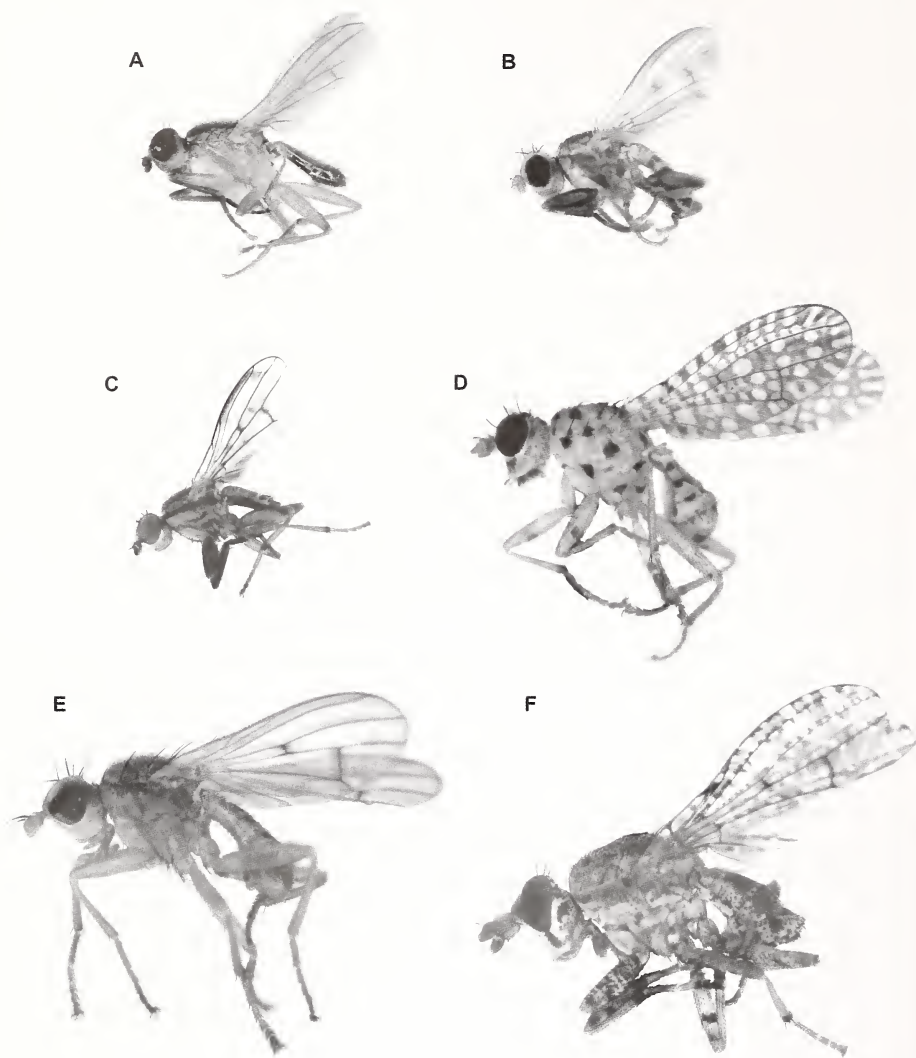


Figure 2. Sciomyzidae adults, lateral view. A, *Pteromicra* sp.; B, *Pherbellia* sp.; C, *Pherbellia nana nana*; D, *Poecilographa decora*; E, *Renocera brevis*; F, *Dictya* sp.

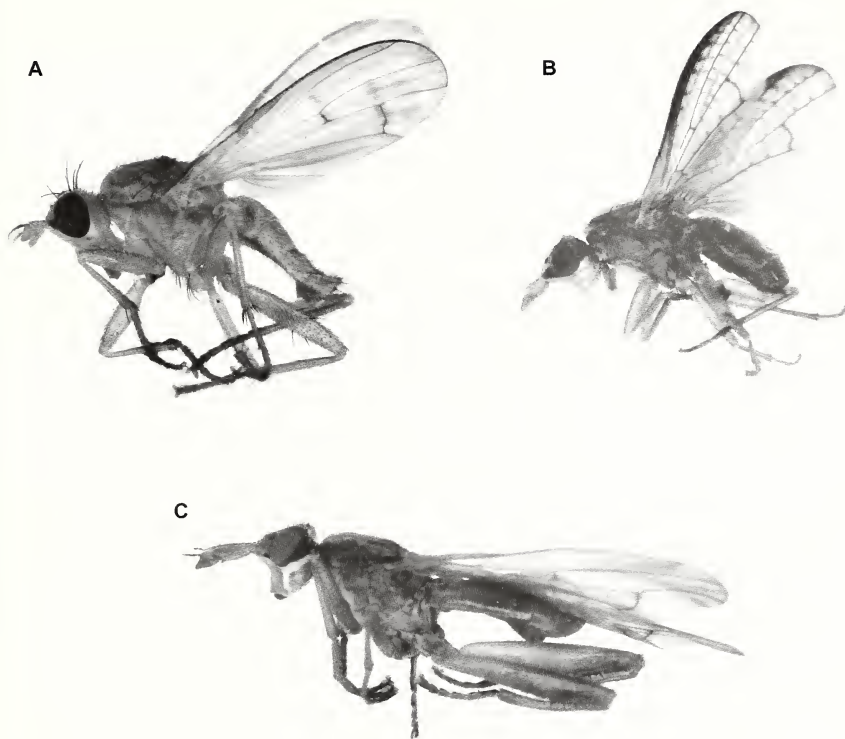


Figure 3. Sciomyzidae adults, lateral view. A, *Tetanocera plebeja*; B, *Limnia* sp.; C, *Sepedon* sp.

	variable	8			
8(7).	Aedeagus bulbous, pointed apically (Figure 7C)			11(10').	Aristal hairs long, plumose; hind coxa with a few hairs on dorsal apex; surstylus slightly curved in lateral view, gonite bilobed (Figure 7F)
 <i>P. paludum</i> Orth			 <i>P. seticoxa</i> Steyskal*
8'.	Aedeagus tri-lobed apically (Figure 7D)			11'.	Aristal hairs moderate to long; hind coxa bare on dorsal apex; male genitalia variable
 <i>P. propages</i> Steyskal*				12
9(4).	Anepisternum with minute hairs over at least most of posterior half, or only along posterior margin	10		12(11').	Gonite tri-lobed apically (Figure 8A)
				 <i>P. quadrata</i> Steyskal
9'.	Anepisternum bare	13		12'.	Gonite lacking lobes apically (Figure 8B)
10(9).	Wing with pale yellow costal border; veins Sc, R ₁ , and R ₂₊₃ yellow; arista short, plumose; surstylus slightly curved and narrow in lateral view (Figure 7E) <i>P. griseola</i> (Fallén)*
 <i>P. albocostata</i> (Fallén)			13(9').	Halter black; arista nearly bare; small blackish species
10'.	Wing hyaline; all veins brown; male genitalia variable	11		 <i>P. luctifera</i> (Loew)*
				13'.	Halter yellow or white; other characters variable
					14

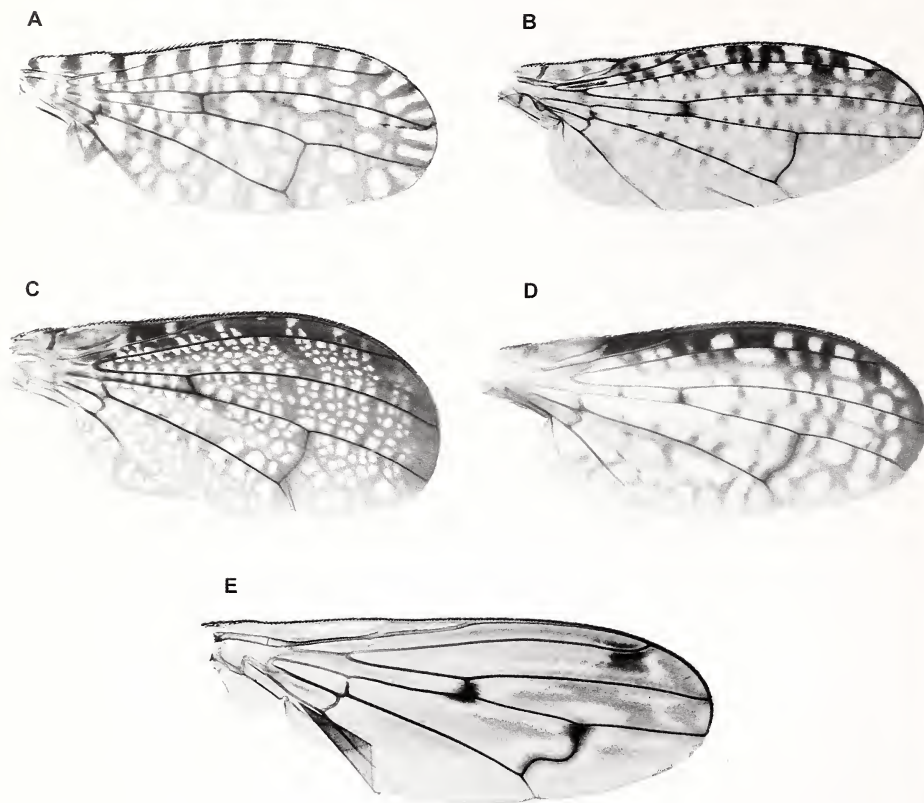


Figure 4. Right wing of adults, dorsal view. A, *Poecilographa decora*; B, *Dictya* sp.; C, *Euthycera arcuata*; D, *Trypetoptera canadensis*; E, *Elgiva sollicita*.

- | | | | | |
|----------|---|----|-------------------|---|
| 14(13'). | Orbito-antennal spot lacking or indistinct; arista short-plumose; anepisternal stripe extending below middle posteriorly; fore legs not contrasting sharply with middle and hind legs | 15 | (Figure 8C) | <i>P. argyra</i> Verbeke |
| 14'. | Orbito-antennal spot present (cf., Figure 1E); arista pubescent or short-plumose; anepisternal stripe not extending below middle posteriorly; fore legs dark, often nearly black, contrasting with light colored middle and hind legs | 16 | 15'. | Anterior margin of frons with whitish yellow to yellow pubescence, with some grayish coloration at anterolateral corners; anepisternal stripe faint, extending below middle, but not reaching lower posterior corner; surstylus large and bulging basally (Figure 8D) |
| 15(14'). | Anterior margin of frons grayish; anepisternal stripe reaching lower posterior corner; surstylus narrow | | | <i>P. anubis</i> Knutson* |
| | | | 16(14'). | Arista pubescent, with most hairs no longer than basal diameter of arista |
| | | | | <i>P. vitalis</i> (Cresson)* |
| | | | 16'. | Arista short-plumose |
| | | | | <i>P. similis</i> (Cresson)* |

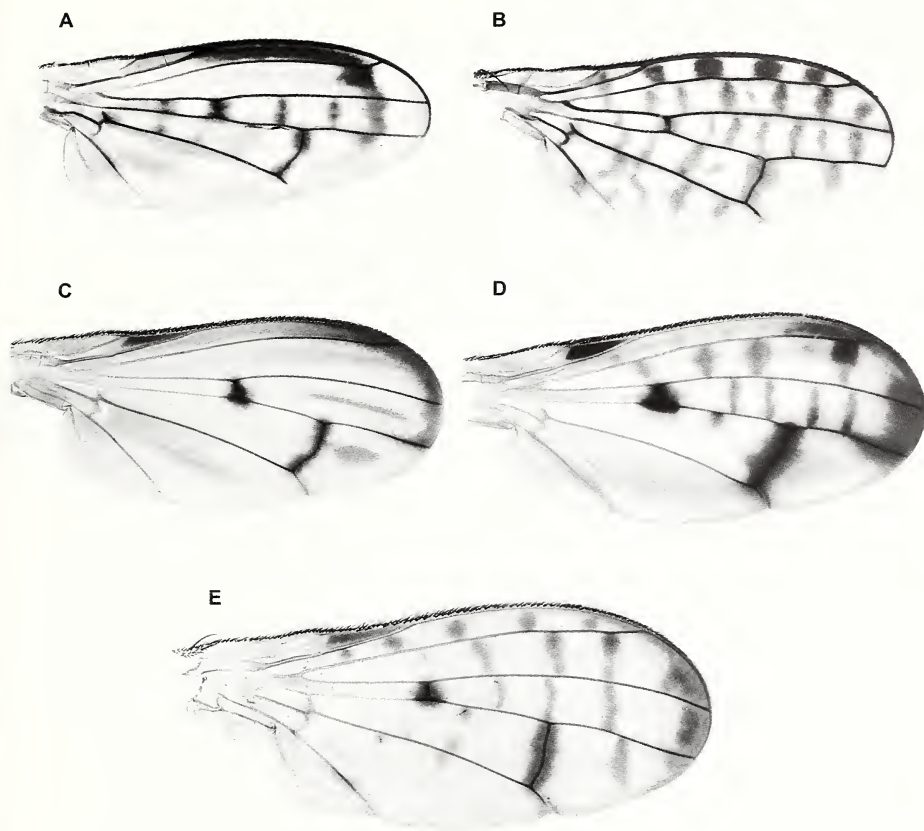


Figure 5. Right wing of adults, dorsal view. A, *Pherbellia nana nana*; B, *P. schoenherri maculata*; C, *Tetanocera plebeja*; D, *T. valida*; E, *T. clara*.

Key to Species of *Sciomyza* Fallén

1. Thoracic dorsum black; anepisternum bare posteriorly; fore femora black, at least on apical half *S. varia* (Coquillett)*
- 1'. Thoracic dorsum ferruginous to grayish; anepisternum with at least a few bristles posteriorly near suture 2
- 2(1'). Palpi blackish, at least apically; center of face strongly blackened; fore femur wholly yellow

- *S. aristalis* (Coquillett)*
- 2'. Palpi wholly yellow; face uniformly yellowish to reddish-brown *S. simplex* Fallén

Key to Species of *Antichaeta* Haliday

1. Scutellum with 2 bristles; 1 pair of dorsocentral bristles *A. johnsoni* (Cresson)
- 1'. Scutellum with 4 bristles; 2 pairs of dorsocentral

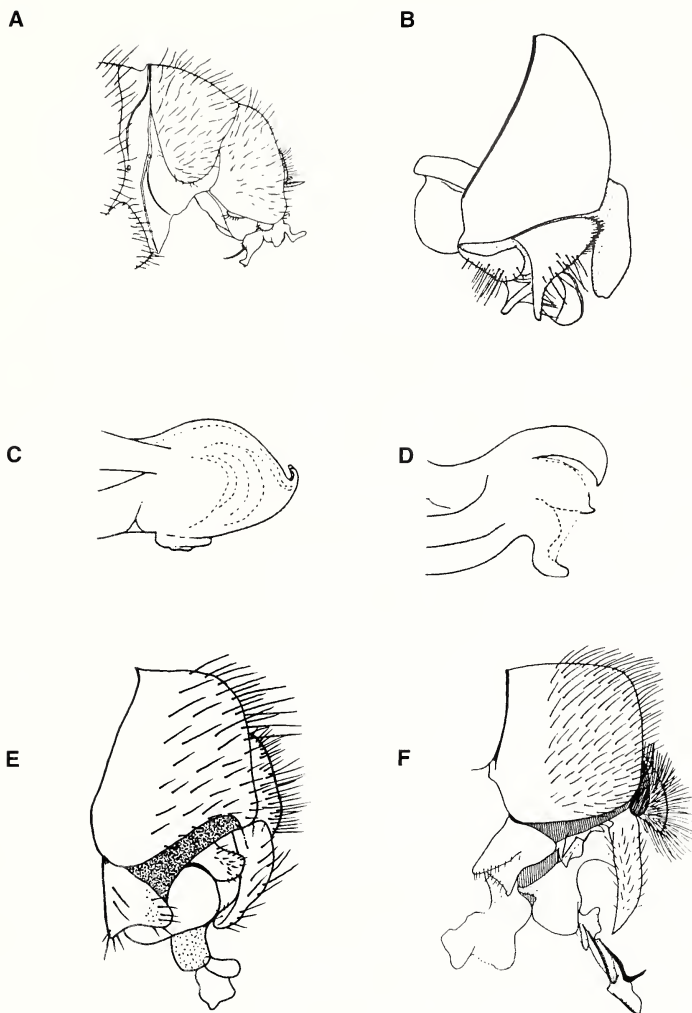


Figure 7. *Phorbettia* species male genitalia, lateral view. A, *P. parallela*, figure modified from Fisher and Orth (1983); B, *P. beatrix*, figure modified from Steyskal (1967); C, *P. paludum*, figure modified from Orth (1982); D, *P. propages*, figure modified from Orth (1982); E, *P. albocostata*, figure modified from Steyskal (1961); F, *P. seticoxa*, figure modified from Steyskal (1961).

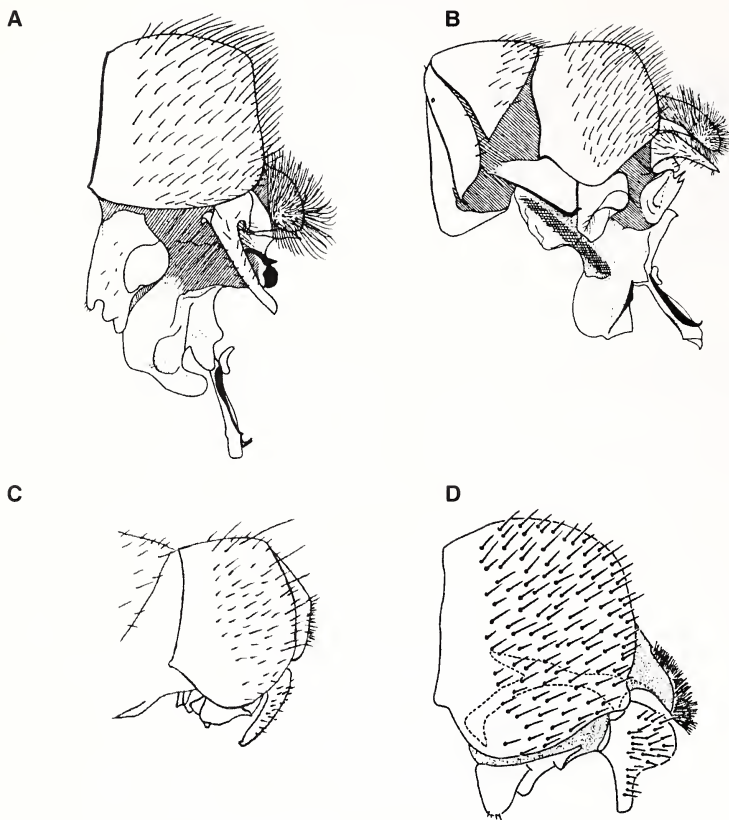


Figure 8. *Pherbellia* species male genitalia, lateral view. A, *P. quadrata*, figure modified from Steyskal (1961); B, *P. griseola*, figure modified from Steyskal (1961); C, *P. argyra*, figure modified from Fisher and Orth (1983); D, *P. anubis* figure modified from Bratt et al. (1969).

- 3(2'). Prescutellar bristles present; arisal hairs long, loosely plumose *R. amanda* Cresson*
 3'. Prescutellar bristles absent; arisal hairs short, dense, and black *R. longipes* (Loew)*

Key to Species of *Dictya* Meigen

1. Ventral process of hypandrium with preterminal lobe (cf. Figure 9A) 2
 1'. Ventral process of hypandrium lacking preterminal lobe, tapering apically 7
 2(1'). Dorsal tip of surstylus with long, stiff bristles; hypandrium as in Figure 9A *D. pictipes* (Loew)*
 2'. Dorsal tip of surstylus lacking stiff bristles 3
 3(2'). Surstylus with dorsal tip strongly projecting, angulate; hypandrium as in Figure 9B *D. hudsonica* Steyskal*
 3'. Surstylus with dorsal tip weakly projecting, rounded; hypandrium variable 4

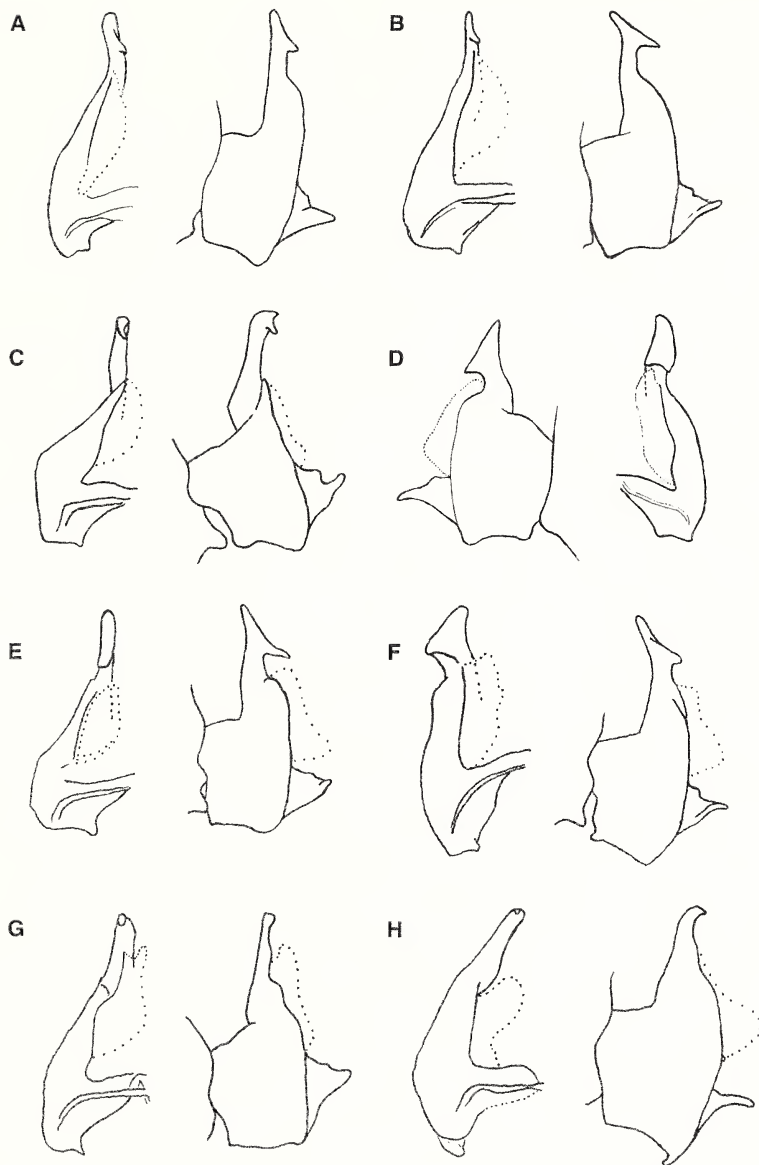


Figure 9. *Dictya* species hypandrium of male genitalia, ventral (left) and lateral (right) views. A, *D. pictipes*; B, *D. hudsonica*; C, *D. sabroskyi*; D, *D. expansa*; E, *D. stricta*; F, *D. atlantica*; G, *D. borealis*; H, *D. laurentia*. All figures modified from Orth (1991).

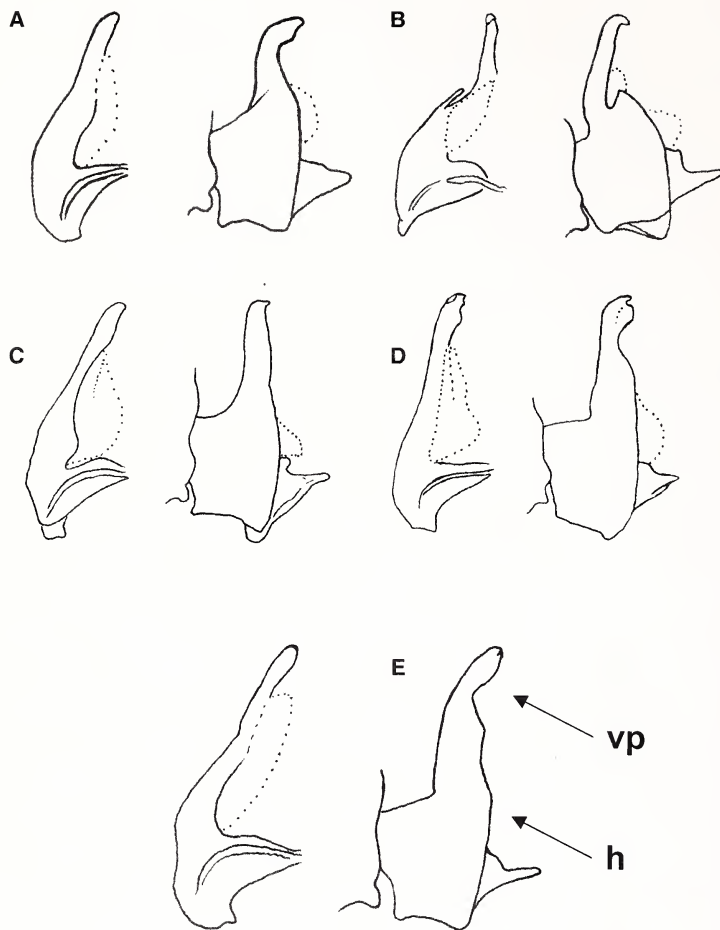


Figure 10. A, *D. umbroides*; B, *D. brimleyi*; C, *D. gaigei*; D, *D. steyskali*; E, *D. texensis*; h = hypandrium, vp = ventral process of hypandrium. All figures modified from Orth (1991).

- | | | | |
|--------|--|-------------------------------|--|
| 4(3'). | Hypandrium with small preterminal lobe (Figure 9C) | <i>D. sabroskyi</i> Steyskal* | 6 |
| 4'. | Hypandrium with large preterminal lobe | 5 | |
| 5(4'). | Ventral process of hypandrium bent forward in lateral view (Figure 9D) | <i>D. expansa</i> Steyskal* | |
| 5'. | Ventral process of hypandrium vertical or nearly so | 6 | |
| | | 6(5'). | Preterminal lobe of hypandrium directed anteriorad (Figure 9E) |
| | | | <i>D. stricta</i> Steyskal* |
| | | 6'. | Preterminal lobe of hypandrium directed laterad (Figure 9F) |
| | | | <i>D. atlantica</i> Steyskal* |
| | | 7(1'). | Surstylus with tip forming a lobe bearing a tuft of |

- long, stiff bristles; hypandrium as in Figure 9G *D. borealis* Curran* 7'.
- Surstylus with tip not forming a lobe, usually with a few short bristles 8
- 8(7'). Surstylus with dorsal tip strongly to moderately projecting, usually angulate 9
- 8'. Surstylus with dorsal tip weakly or slightly projecting, usually rounded 10
- 9(8). Hypandrium long, hooked at tip in ventral view (Figure 9H) *D. laurentiana* Steyskal
- 9'. Hypandrium short, curved (Figure 10A) *D. umbroides* Curran
- 10(8'). Basal area of hypandrium with anterior emargination (Figure 10B) *D. brimleyi* Steyskal
- 10'. Basal area of hypandrium lacking anterior emargination 11
- 11(10'). Hypandrium with a thin anterior flange 12
- 11'. Hypandrium lacking flange (Figure 10C) *D. gaigei* Steyskal
- 12 (11). Distal tip of hypandrium with deep notch and hook (Figure 10D) *D. steyskali* Valley*
- 12'. Distal tip of hypandrium with shallow notch and lacking hook (Figure 10E) *D. texensis* Curran*

Key to Species of *Tetanocera* Duméril

1. Posterior surface of middle femur with 2–3 subapical bristles; prosternum bare or sparsely haired; dark orbito-antennal spot lacking 2
- 1'. Posterior surface of middle femur with 1 subapical bristle, or bristles lacking; prosternum bare; dark orbito-antennal spot present (cf., Figure 1E) 3
- 2(1). Prosternum sparsely haired; posterior femur with dorsal bristles on anterior side only; male genitalia as in Figure 11A *T. robusta* Loew
- 2'. Prosternum bare; posterior femur with posterodorsal preapical bristle; male genitalia as in Figure 11B *T. amae* Steyskal*
- 3(1'). Posterior surface of middle femur with single subapical bristle; crossvein dm-cu strongly S-curved 4
- 3'. Posterior surface of middle femur with small hairs only; crossvein dm-cu variable 8
- 4(3). Parafacial area with hairs well above half-way between lower margin of eye and border of antennal socket 5
- 4'. Parafacial area with hairs extending less than halfway from lower margin of eye to border of antennal socket 7
- 5(4). R₄₊₅ lacking stump veins; surstylus as in Figure 11C *T. plumosa* Loew*
- 5'. R₄₊₅ with stump veins; surstylus as in Figures 11D and 11E 6
- 6(5'). Surstylus tapered and slightly hooked apically (Figure 11D) *T. vicina* Macquart*
- 6'. Surstylus rounded and not hooked apically (Figure 11E) *T. iowensis* Steyskal*
- 7(4'). Arista plumosity dense and black; blackish orbito-antennal spot present; wings with strong costal browning; surstylus curved to an acute point (Figure 11F) *T. loewi* Steyskal*
- 7'. Arista plumosity sparse; orbito-antennal spot faint or lacking; surstylus bent apically forming a point (Figure 12A) *T. mesopora* Steyskal
- 8(3'). Hind femur with posterodorsal bristle, opposite or nearly opposite to apical anterodorsal bristle; arista plumosity long but sparse 9
- 8'. Hind femur lacking posterodorsal bristle; arista plumosity variable 10
- 9(8). Crossvein dm-cu S-curved; male genitalia as in Figure 12B *T. montana* Day*
- 9'. Crossvein dm-cu straight or nearly so; male genitalia as in Figure 12C *T. rotundicornis* Loew*
- 10(8'). Wing with heavy pattern; interfrontal stripe broad and polished 11
- 10'. Wing lacking heavy pattern; interfrontal stripe variable 12
- 11(10). Both sides of M₁₊₂ with spots; surstylus triangular in lateral view (Figure 12D); wing darkly spotted (Figure 5D) *T. valida* Loew*
- 11'. No spots along M₁₊₂; surstylus narrow and sickle-shaped in lateral view (Figure 12E); spotting of wing moderately dark (Figure 5E) *T. clara* Loew*
- 12(10'). Interfrontal stripe not sharply demarcated, forming broad, triangular dullly shining area anterior to ocellus; costal margin not browned; male genitalia as in Figure 13A *T. fuscineris* (Zetterstedt)*
- 12'. Interfrontal stripe more or less parallel sided 13
- 13(12'). Interfrontal stripe narrow, ending well before anterior margin of frons, or indistinct; wings unicolorous; surstylus forming acute triangle in lateral view (Figure 13B) *T. ferruginea* Fallén*
- 13'. Interfrontal stripe robust, extending to or nearly to anterior margin of frons; other characters variable 14
- 14(13'). Interfrontal stripe broad, polished, reaching anterior margin of frons; parafacial stripes also broad and polished; orbito-antennal spot lacking in most specimens; wing tip and crossveins darkened (Figure 5C); surstylus narrow, slightly curved

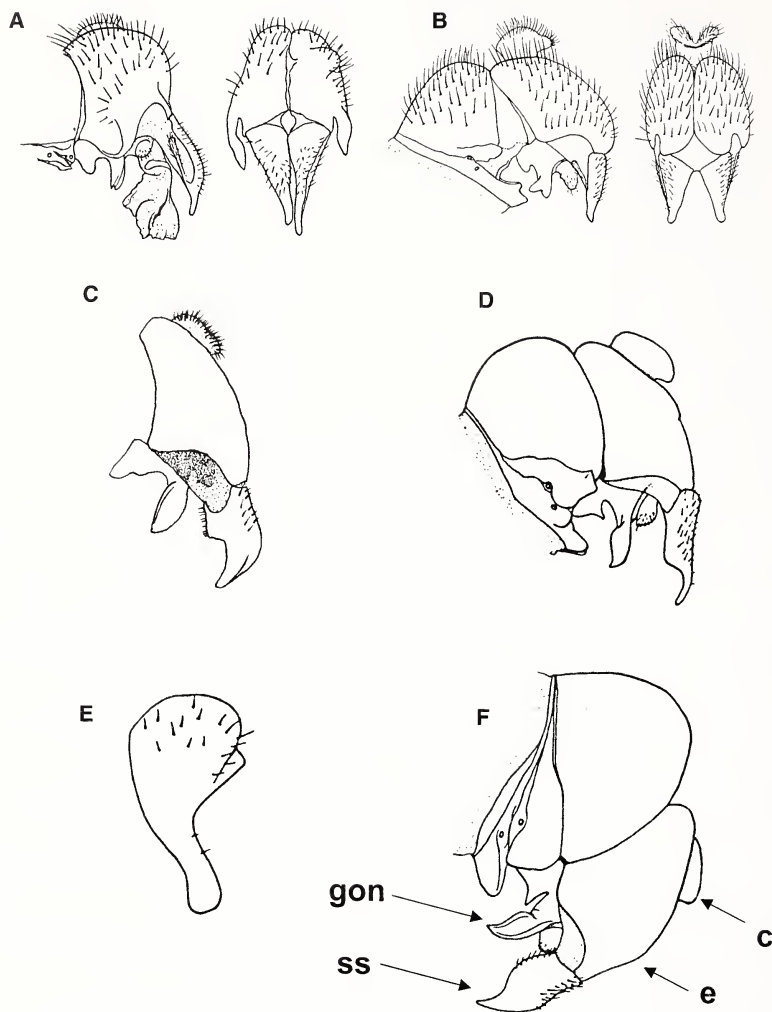


Figure 11. *Tetanocera* species male genitalia. A, *T. robusta*, lateral (left) and ventral (right) views; B, *T. amiae*, lateral (left) and ventral (right) views; C, *T. plumosa*, lateral view; D, *T. vicina*, lateral view; E, *T. iowensis*, lateral view; F, *T. loewi*, lateral view; c = cercus, e = epandrium, gon = gonite, ss = surstylus. All figures modified from Steyskal (1959).

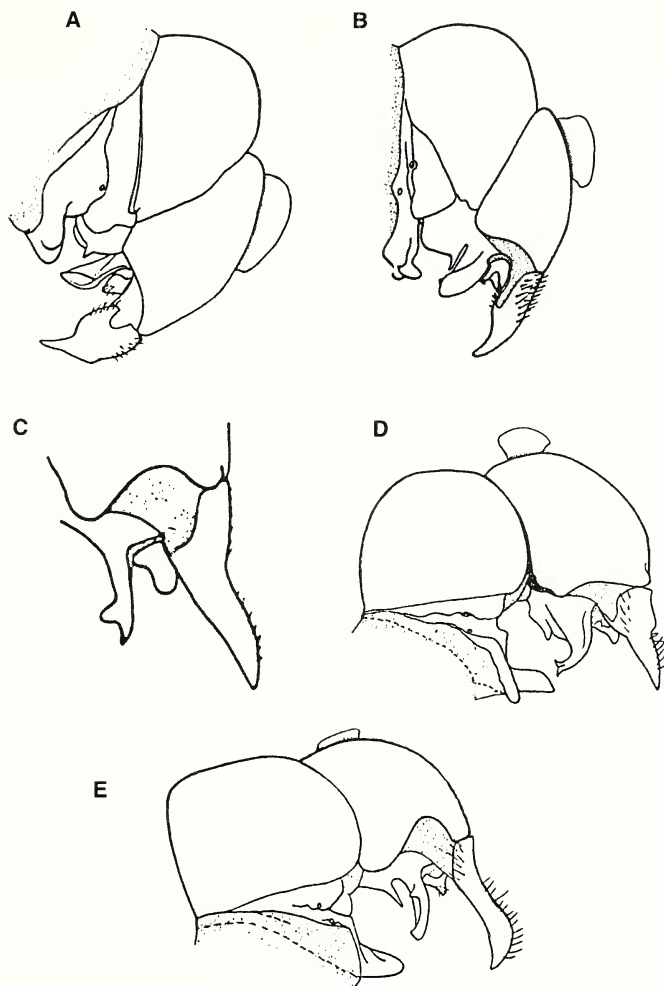


Figure 12. *Tetanocera* species male genitalia, lateral view. A, *T. mesopora*; B, *T. montana*; C, *T. rotundicornis*; D, *T. valida*; E, *T. clara*. All figures modified from Steyskal (1959).

- (Figure 13C) *T. plebeja* Loew*
- 14'. Interfrontal and parafrontal stripes broad but not shining; male genitalia and wing variable 15
- 15(14'). Second antennal segment 1.5 times as high as long; costal margin lacking brown coloration basally; surstylus strongly curved, with strong posterior ridge of hair (Figure 13D)
..... *T. phyllophora* Melander
- 15'. Second antennal segment as high as long; male genitalia variable 16
- 16(15'). Stigma light brown; dorsum of thorax with faint stripes; surstylus broad basally, curving to a point apically (Figure 13E) *T. oxia* Steyskal*
- 16'. Stigma dark brown; thorax lacking stripes; surstylus forming acute, slightly curved triangle (Figure 13F) *T. melanostigma* Steyskal*

Key to Species of *Dictyacium* Steyskal

1. Fore basitarsus whitish, strongly contrasting with dark tibia; mesonotal coloration not forming stripes; facial protuberance occupying less than half the distance from the antennae to oral margin; eye oval *D. ambiguum* (Loew)
- 1'. Fore basitarsus dark, sometimes pale basally, but not contrasting dark tibia; mesonotal coloration tending to form a pair of dorsocentral stripes; facial protuberance occupying half the distance from antennae to oral margin; eye round
..... *D. firmum* Steyskal

Key to Species of *Limnia* Robineau-Desvoidy

1. Frons with polished area in anterior outer corner 2
- 1'. Frons lacking polished area in anterior outer corner 4
- 2(1). Wing pattern denser anteriorly than posteriorly (Figure 6A); posterior surstylus narrow, relatively straight; anterior surstylus curved anteriorly (Figure 14A) *L. loewi* Steyskal*
- 2'. Wing pattern uniformly dense; male genitalia various 3
- 3(2). Male genitalia as in Figure 14B; costal margin of wing uniformly dark *L. sandovalensis* Fisher and Orth*
- 3'. Male genitalia as in Figure 14C; costal margin of wing adorned with spots (Figure 6B)
..... *L. boscii* (Robineau-Desvoidy)*
- 4(1'). Second antennal segment swollen laterally, usually adorned with black spot of variable size; male genitalia as in Figure 14D *L. shamoni* Cresson*

- 4'. Second antennal segment not swollen, lacking black spot; male genitalia variable 5
- 5(4'). Hypandrium bifid at apex, with two moderate or very small lobes 6
- 5'. Hypandrium not bifid 7
- 6(5). Hypandrium slender, straight, with two moderately large apical lobes (Figure 14E); costal margin darkened narrowly (Figure 6C) *L. fitchi* Steyskal*
- 6'. Hypandrium hooked apically, lacking lobes (Figure 14F); costal margin of wing darkened more broadly *L. nambai* Steyskal*
- 7(5'). Surstylus conical; hypandrium hooked apically, broader basally (Figure 15A); prosternum bare; wing with dark costal margin (Figure 6D)
..... *L. conica* Steyskal*
- 7'. Not matching above description 8
- 8(7'). Prosternum with three or more pairs of setae; surstylus in profile strongly curved forming rounded apical tooth; hypandrium strongly curved forming a rounded hook (Figure 15B)
..... *L. lindbergt* Steyskal
- 8'. Not matching above description 9
- 9(8'). Hypandrium with apical hook rounded, short; surstylus roughly rectangular (Figure 15C)
..... *L. georgiae* Melander*
- 9'. Not matching above description 10
- 10(9'). Hypandrium with strongly recurved, short apical hook; surstylus broadly triangular (Figure 15D); wing pattern as in Figure 6E *L. ottawensis* Melander*
- 10'. Hypandrium broadly curved, forming squat hook shape; surstylus rectangular with small pointed process on antero-ventral corner (Figure 15E); wing pattern otherwise *L. septentrionalis* Melander*

Key to Species of *Elgiva* Meigen

1. Wing with dark spot near apex; surstylus with triangular process on anterior margin (Figure 16A); not recorded from Ohio *E. connexa* (Harris)
- 1'. Wing without dark spot near apex (Figure 4E); surstylus with small bulge and adjacent indentation on anterior margin (Figure 16B); common
..... *E. sollicita* (Steyskal)*

Key to Species of *Sepedon* Latreille

1. Katatergite callus with black setae 2
- 1'. Katatergite callus lacking black setae 7
- 2(1). Medifacies with fine black setae; katatergite callus densely setose 3

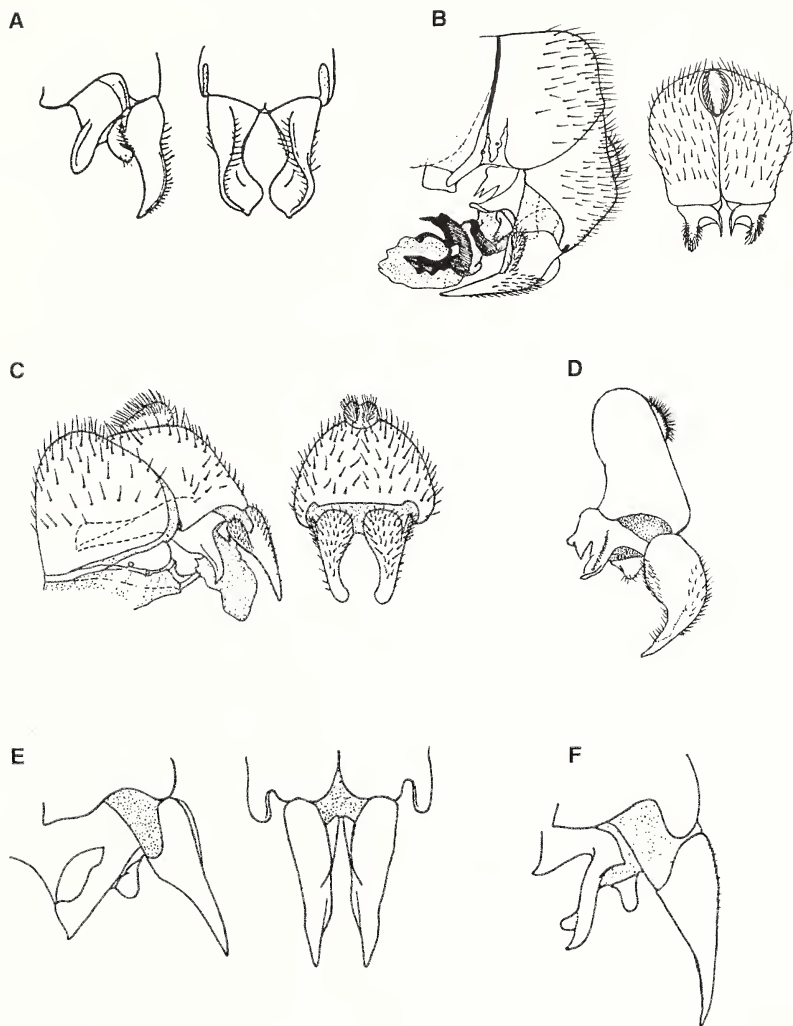


Figure 13. *Tetanocera* species male genitalia. A, *T. fuscinervis*, lateral (left) and ventral (right) views; B, *T. ferruginea*, lateral (left) and ventral (right) views; C, *T. plebeja*, lateral (left) and ventral (right) views; D, *T. phyllophora*, lateral view; E, *T. oxia*, lateral view (left) and ventral (right); F, *T. melanostigma*, lateral view. All figures modified from Steyskal (1959).

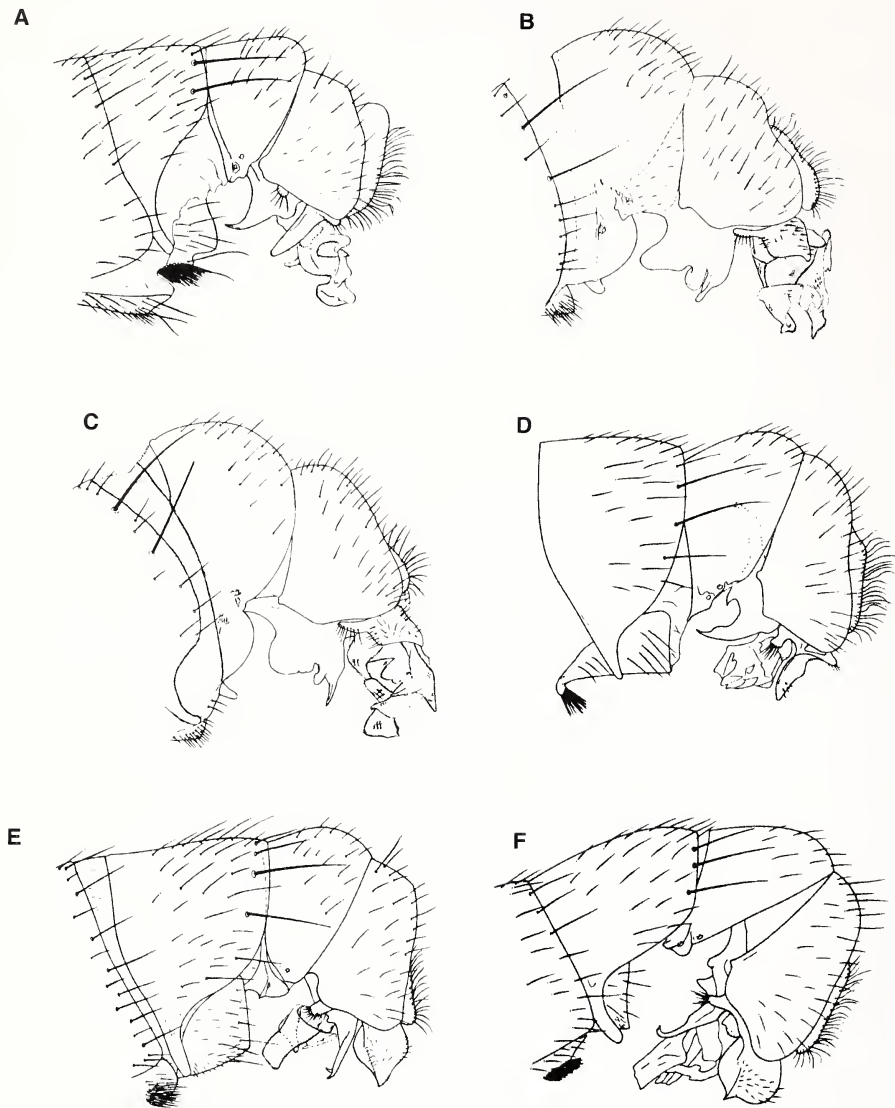


Figure 14. *Linnia* species male genitalia, lateral view. A, *L. loewi*; B, *L. sandovalensis*; C, *L. boscii*; D, *L. shannoni*; E, *L. fitchi*; F, *L. nambai*. All figures modified from Steyskal et al. (1978).

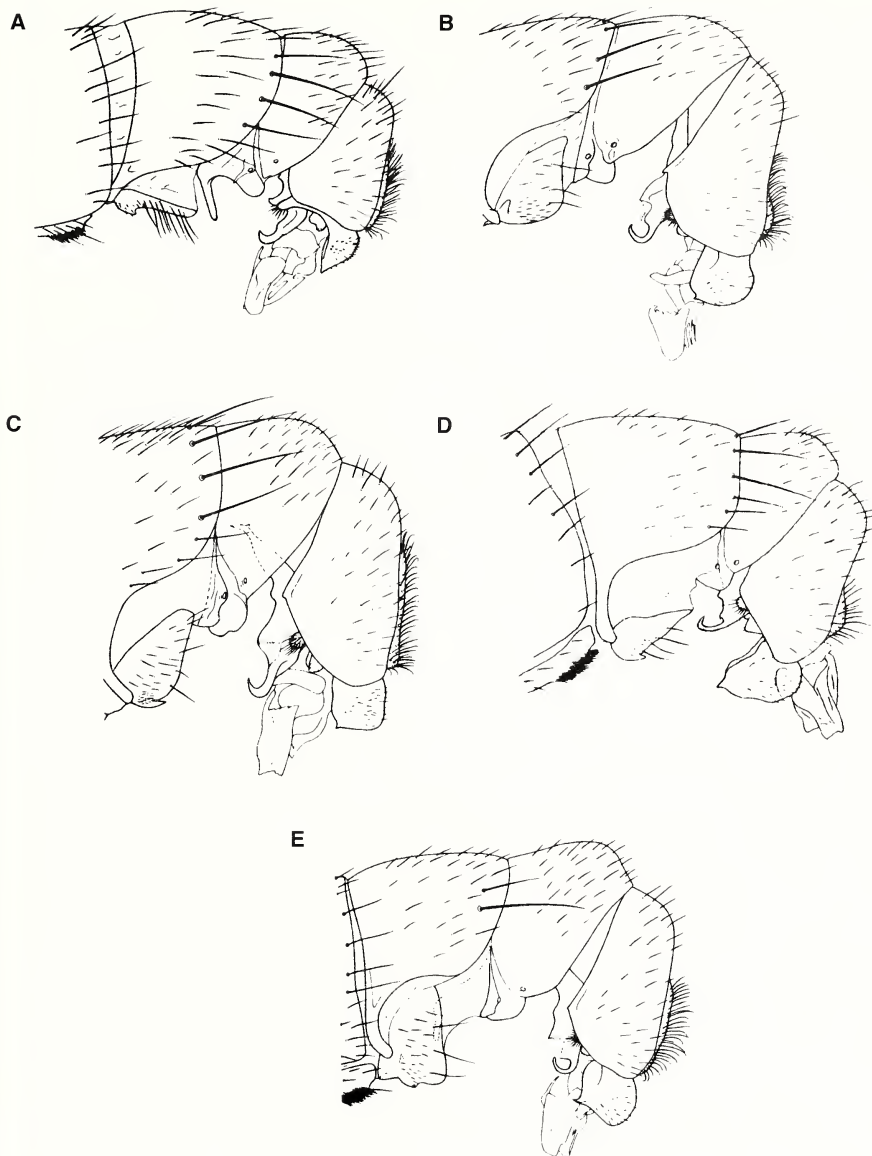


Figure 15. *Linnia* species male genitalia, lateral view. A, *L. conica*; B, *L. lindbergi*; C, *L. georgiae*; D, *L. ottawensis*; E, *L. septentrionalis*. All figures modified from Steyskal et al. (1978).

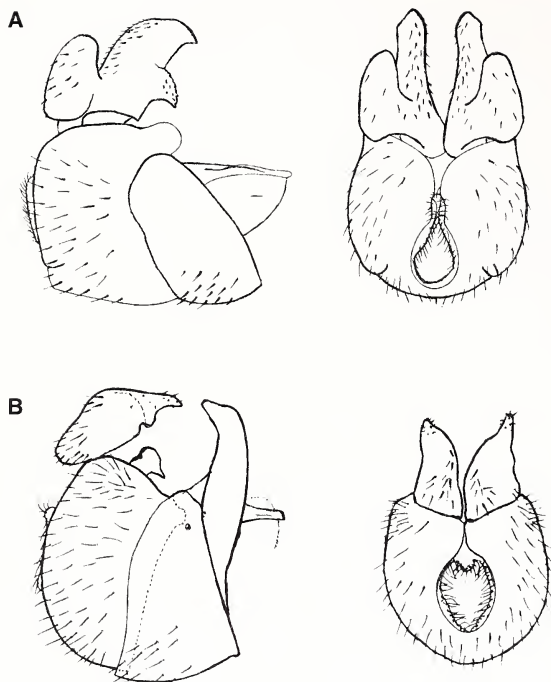


Figure 16. *Elgiva* species male genitalia. A, *E. comexa*, lateral (left) and ventral (right) views; B, *E. sollicita*, lateral (left) and ventral (right) views. Figures modified from Orth and Knutson (1987).

2'. Medifacies lacking fine black setae; katatergite cal- lus sparsely setose <i>S. spinipes americana</i> Steyskal*	6'. Light-colored species; fronto-orbital spots small <i>S. pusilla</i> Loew*
3(2). Hind femur of male with deep indentation on ven- tral surface (Figure 1D); small species <i>S. armipes</i> Loew*	7(1'). Second antennal segment approximately 2.5 times as long as wide in lateral view; frons with distinct, velvety fronto-orbital black spot <i>S. fuscipennis fuscipennis</i> Loew*
3'. Hind femur of male lacking deep indentation on ventral surface; size variable 4	7'. Second antennal segment 4 or more times as long as wide in lateral view; fronto-orbital spot variable 8
4(3'). Median stripe of pruinosity on face extending in a point to oral margin 5	8(7'). Second antennal segment about 4 times longer than wide <i>S. gracilicornis</i> Orth*
4'. Median stripe of pruinosity on face not reaching oral margin 6	8'. Second antennal segment about 5 times longer than wide <i>S. tenuicornis</i> Cresson*
5(4). Oral margin generally low, in profile angle with face acute <i>S. neilli</i> Steyskal*	
5'. Oral margin raised, in profile angle with face approximately at right angle. <i>S. lignator</i> Steyskal*	
6(4'). Dark-colored species; fronto-orbital spots large <i>S. borealis</i> Steyskal*	

Annotated List of Ohio Species

The following list provides data on the Nearctic distribution of each species recorded from Ohio, a detailed list of Ohio records, and general information on each species' habitat, phenology, biology, and immature stages that are described in the

literature. **General Distribution** gives the distribution for species in Canadian provinces, Mexico, and the United States, or provides a descriptive statement for widely distributed taxa.

Ohio Records provides details from the labels of the specimens examined from which the distribution maps were created. Details of **Habitat** refer to environments where larvae, pupae, and/or adults have been encountered. **Phenology** refers to both immature stages and adults, whereas **Biology** is a synopsis of larval feeding habits. We use the following abbreviations: **Date**, I–XII referring to January–December, respectively; **Immature stages** indicates those life stages described taxonomically in the literature where E = egg, L₁₋₃ = larval instars 1–3, respectively, and P = pupa.

1. *Atrichomelina pubera* (Loew, 1862)

General Distribution: Transcontinental in southern Canada and USA south to Chiapas, Mexico.

Ohio Records (Figure 17A): **Ashtabula**, Conneaut Creek, reared from puparium on unionid mussel shell, V-04-1996, J. K. Bissell, 2♂, 3♀ (CMNH); **Champaign**, Cedar Swamp, X-08-1963, J. L. Williams, (OSU); **Franklin**, Columbus, III-04-1897, J. S. Hine (OSU); **Fulton**, Wauseon, VIII-29-1920, J. S. Hine (OSU); **Lake**, Mentor Marsh, VI-08-1981, A. D. Huryn, 1♂ (CMNH); Mentor Marsh, V-30-2001, J. B. Keiper, 1♂ (CMNH); **Ottawa**, Put-in-Bay VI-18-1934, R. C. Osburn (OSU); **Portage**, 1 mile N Kent, III-20-1962, B. A. Foote, 1♂ reared from puparium (CMNH), 2.5 miles E Kent, VIII-18-1996, J. B. Keiper, 1♂ (CMNH); 10 miles E Kent, IV-25-1963, B. A. Foote (CMNH); **Wayne**, 0.5 miles S Rittman, IX-09-1969, B. A. Foote (CMNH).

Habitat: Marshes, wooded swamps, buttonbush swamps, fens, riparian areas.

Phenology: Multivoltine. Overwinters either as pupa in shell of prey snail or away from shell.

Biology: Predator/scavenger of stranded pulmonate aquatic snails (Foote et al., 1960).

Immature Stages: E, L₁₋₃, P (Foote et al., 1960).

2. *Oidematops ferrugineus* Cresson, 1920

General Distribution: PQ: GA, KS, ME, MI, MO, NH, NY, OH, VT.

Ohio Records (Figure 17B): **Columbiana**, Beaver Creek State Park, V-25-2000, B. A. Foote, 1♀ (BAF); **Portage**, 4.5 miles E Kent, III-20-1966, B. A. Foote, 1♂ reared from puparium in shell of *Stenotrema hirsutum* (Say) (CMNH); VI-06-1967, K. Valley, 4♀ (CMNH).

Habitat: Floodplain forests.

Phenology: Univoltine. Flight period from late May to early June. Biology: Larva parasitoid in the land snail *Stenotrema hirsutum* (Say) (Foote, 1977).

Immature Stages: None described.

3. *Pherbellia albovarva* (Coquillett, 1901)

General Distribution: Southeastern Canada and northeastern USA south to NC.

Ohio Records (Figure 17C): **Portage**, Jennings Woods NE of Ravenna, V-23-1972, 1♂ reared from puparium in the land snail *Anguispira alternata* (Say) (CMNH).

Habitat: Beech-maple forests.

Phenology: Univoltine. Flight period in Ohio occurs in late May. Overwintering takes place as pupa within the shell of host snail.

Biology: Larvae prey on land snails belonging to the genera *Anguispira*, *Discus*, *Triodopsis*, and *Zonitoides* (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

4. *Pherbellia anubis* Knutson, 1969 (*in* Bratt et al., 1969)

General Distribution: PQ: AK, MT, MN, MI, NY, OH.

Ohio Records (Figure 17D): **Portage**, 4.5 miles E Kent, VI-03-1968, B. A. Foote, 2♂ (CMNH).

Habitat: Marshes.

Phenology: Bi- or trivoltine. Flight period in Ohio occurs in early June. Overwintering occurs as pupa in shoreline leaf litter or occasionally in shell of host snail.

Biology: Larvae prey on pulmonate aquatic snails that have been exposed on shorelines by dropping water levels (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

5. *Pherbellia beatricis* Steyskal, 1949

General Distribution: ONT: IN, MI, MS, OH.

Ohio Records (Figure 17E): **Champaign**, Cedar Swamp, V-22-1954, R. E. Woodruff, 2♂ (FSCA); VI-17-1961, B. A. Foote, 8♂, 1♀ (CMNH); V-21-1964, B. A. Foote, 18♂, 12♀ (CMNH); VII-24-1964, J. L. Williams, 6♂ (OSU); VIII-17-1964, J. L. Williams, 8♂ (OSU); IX-15-1964, J. L. Williams, 1♂ (OSU); IX-16-1965, J. L. Williams, 15♂, 4♀ (OSU); X-08-1963, J. L. Williams, 1♂ (OSU).

Habitat: Fens.

Phenology: Trivoltine. Flight period occurs in Ohio from late May to early October. Overwintering habits unknown.

Biology: Larvae prey on stranded aquatic snails belonging to the genera *Aplexa* and *Physa* (Bratt et al., 1969).

Immature Stages: L₁₋₂ (Bratt et al., 1969).

6. *Pherbellia griseola* (Fallén, 1820)

General Distribution: Transcontinental in Canada and USA.

Ohio Records (Figure 17F): **Portage**, 7.0 miles E Kent, V-07-1962, B. A. Foote, 4♂, 4♀ (CMNH); 7.0 miles E Kent, V-13-1962, B. A. Foote, 10♂ (CMNH); 1.0 mile N Kent, VI-01-1963, B. A. Foote, 1♂, 1♀ (CMNH).

Habitat: Marshes, woodland vernal pools, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from early May to early June. Overwintering occurs as pupa in shell of host snail.

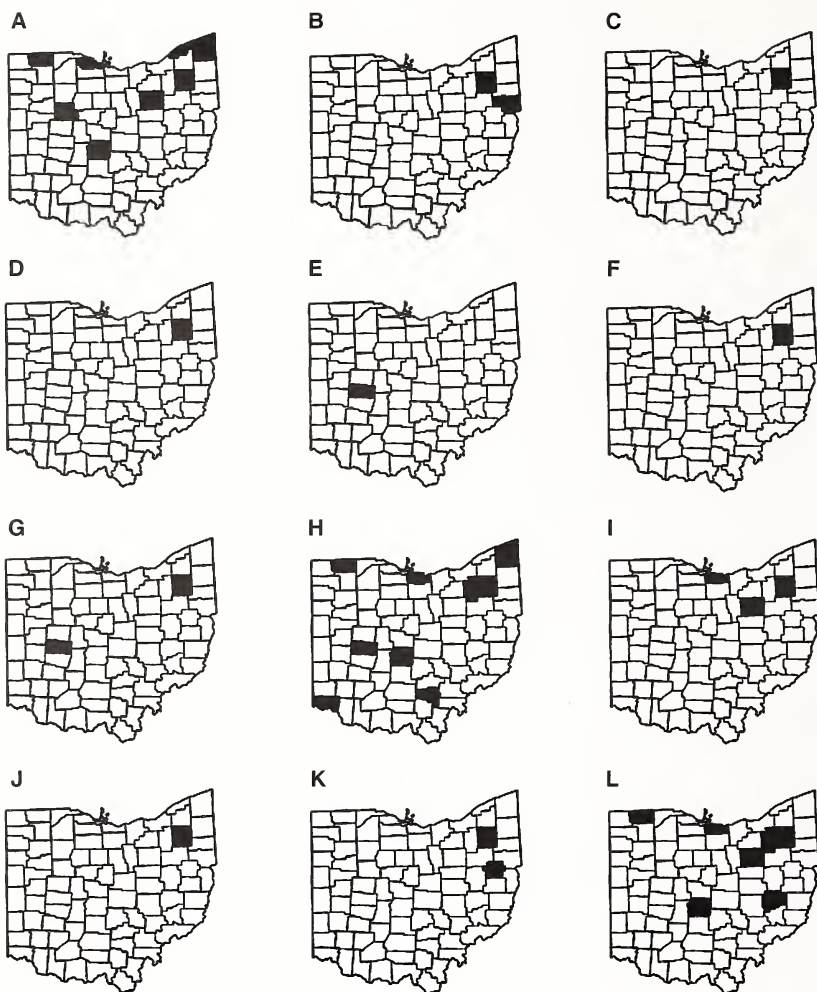


Figure 17. Distribution of Ohio Sciomyzidae. A, *Atrichomelina pubera*; B, *Oidematomys ferrugineus*; C, *Pherbellia albovarva*; D, *Pherbellia anubis*; E, *Pherbellia beatricis*; F, *Pherbellia griseola*; G, *Pherbellia lucifera*; H, *Pherbellia nana*; I, *Pherbellia parallela*; J, *Pherbellia propages*; K, *Pherbellia schoenherri maculata*; L, *Pherbellia seticoxa*.

Biology: Larvae prey on stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

7. *Pherbellia luctifera* (Loew, 1861)

General Distribution: NF, ON, PQ; IA, IN, NY, OH, PA.

Ohio Records (Figure 17G): **Champaign**, Cedar Swamp, R. E. Woodruff, 1♂ (CMNH); **Portage**, 1 mile E Kent, IV-29-1976, B. A. Foote, 1♀ (CMNH).

Habitat: Fens, marshes.

Phenology: Voltinism unknown. Flight period in Ohio is in late April. Overwintering habits are unknown.

Biology: Unknown.

Immature Stages: None described.

8. *Pherbellia nana nana* (Fallén, 1820)

General Distribution: Transcontinental in North America.

Ohio Records (Figure 17H): **Ashtabula**, Pymatuning Creek Fen, VI-21-2001, J. B. Keiper, 1♀ (CMNH); **Champaign**, Cedar Swamp, V-21-1964, B. A. Foote, 1♀ (CMNH); **Erie**, Sandusky, VII-15-1907, J. S. Hine, 1♂ (OSU); **Franklin**, Columbus, V-15-1902, J. S. Hine (OSU); **Fulton**, Wauseon, VIII-25 to 29-1902, J. S. Hine, 6 (OSU); IX-04-1902, J. S. Hine, 3♂ (OSU); **Hamilton**, Cincinnati, IX-04-1974, W. Downing 1♀ (CMNH); **Portage**, 7 miles E Kent, V-07-1962, B. A. Foote, 1♀ (CMNH), 1.0 mile E Kent, V-14-1962, B. A. Foote, 2♂ (CMNH); Wingfoot Lake, IX-08-1961, B. A. Foote, 1♂ (CMNH); **Summit**, Akron, V-21-1899, J. S. Hine, 1♂ (OSU); **Barberton**, VIII-01-1996, 1♂, 1♀, J. B. Keiper (CMNH); Cuyahoga Valley National Park (then Cuyahoga Valley National Recreation Area), VII-10-1998, B. A. Foote, 1♂ (CMNH); alkaline area near Barberton, VIII-26-1997, J. B. Keiper, 1♂ (CMNH); **Vinton**, VI-05-12-1900, J. S. Hine, 1♂ (OSU).

Habitat: Marshes, swamps, margins of lakes, roadside drainage ditches.

Phenology: Multivoltine. Flight period in Ohio occurs from early May to early September. Overwinters as pupa in the shell of host snail or in leaf litter.

Biology: Larvae prey on stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt, et al., 1969).

9. *Pherbellia parallela* (Walker, 1853)

General Distribution: Transcontinental in Canada and USA south to Costa Rica.

Ohio Records (Figure 17I): **Erie**, Sandusky, VII-15-1907, J. S. Hine, 1♀ (OSU); **Portage**, cemetery in north Kent, IX-1961, B. A. Foote, 1♂ (CMNH); 1.0 mile N Kent, V-14-1962, B. A. Foote, 3♂ (CMNH); **Wayne**, 0.5 mile S Rittman, IX-09-1969, B. A. Foote, 2♂ (CMNH).

Habitat: Marshes, open mud flats, vernal ponds, drainage ditches.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-May to mid-September. Overwinters as pupa in leaf litter or in shell of host snail.

Biology: Predator of stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

10. *Pherbellia propages* Steyskal, 1967

General Distribution: AB, MB, NWT, SK; AK, ND east to OH. Ohio Records (Figure 17J): **Portage**, 7.0 miles E Kent, V-13-1962, B. A. Foote, 2♂ (CMNH).

Habitat: Marshes.

Phenology: Multivoltine. Recorded in Ohio only in mid-May. Overwinters as pupa in leaf litter.

Biology: Larvae prey on stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₃, P (Bratt et al., 1969).

11. *Pherbellia schoenherri maculata* (Cresson, 1920)

General Distribution: Transcontinental in North America.

Ohio Records (Figure 17K): **Carroll**, 3.0 miles E Carrollton, VII-17-1964, R. E. Mannell, 1♀ (CMNH); **Portage**, 1.0 mile E Kent, VII-15-2000, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, drainage ditches.

Phenology: Multivoltine. Adults have been recorded in Ohio only in mid-July. Overwinters as pupa in leaf litter or in the shell of host snail.

Biology: Parasitoid on snails of family Succineidae (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

12. *Pherbellia seticoxa* Steyskal, 1961

General Distribution: MN east to PQ, south to MD, west to KS and MT.

Ohio Records (Figure 17L): **Erie**, Cedar Point near Sandusky, VII-07-20-1904, J. S. Hine, 1♀ (OSU); **Franklin**, Columbus, VII-07-1900, J. S. Hine, 1♂ (OSU); **Fulton**, Wauseon, IX-17-1902, J. S. Hine, 1♂, 2♀ (OSU); **Guernsey**, 10 miles S Cambridge, VII-31-1965, R. E. McConnell, 4♂ (CMNH); **Portage**, 7.0 miles E Kent, V-13-1962, B. A. Foote, 7♂ (CMNH); 1.0 miles N Kent, V-13-1962, B. A. Foote, 7♂ (CMNH); **Summit**, Akron, V-21-1899, J. S. Hine, 1♀ (OSU); **Wayne**, 0.5 miles S Rittman, IX-09-1969, B. A. Foote, 4♂ (CMNH).

Habitat: Marshes, vernal woodland pools, ponds.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-May to mid-September. Overwinters as pupa in shell of host snail or in leaf litter.

Biology: Larvae prey on stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

13. *Pherbellia similis* Cresson, 1920

General Distribution: PQ; DC, MA, MI, NY, OH, WI.

Ohio Records (Figure 18A): **Portage**, Dollar Lake near Twin Lakes, IV-24-1963, B. A. Foote, 1♂ (CMNH); 1 mile N Kent, III-20-1962, B. A. Foote, 3♂ reared from puparia in shells of *Planorbula jenkinsii* Carpenter (CMNH); Streetsboro Bog, III-27-1962, B. A. Foote, 1♂ reared from puparium in shell of *P. jenkinsii* (CMNH); 7.0 miles E Kent, V-07-1962, B. A. Foote, 1♂ reared from puparium in shell of *P. jenkinsii* (CMNH); **Wayne**, 0.5 mile S Ritman, IV-24-1963, 1♂ (CMNH).

Habitat: Woodland pools, buttonbush swamps, fens.

Phenology: Univoltine. Flight period in Ohio from late April to late May. Overwinters as pupa within floating shells of the aquatic snail *P. jenkinsii*.

Biology: Parasitoid of the aquatic snail *P. jenkinsii* (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

14. *Pherbellia vitalis* (Cresson, 1920)

General Distribution: AB, BC, ON, AR, CO, ID, MT, OH, UT.

Ohio Records (Figure 18B): **Ashtabula**, Pymatuning Reservoir near Simmons, V-25-1963, B. A. Foote, 1♂ (CMNH); **Portage**, 1.0 mile N Kent, X-23-1963, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from late May to late October. Overwinters as pupa in shell of host snail or occasionally in leaf litter.

Biology: Larvae prey on stranded pulmonate aquatic snails (Bratt et al., 1969).

Immature Stages: E, L₁₋₃, P (Bratt et al., 1969).

15. *Pteromicra pleuralis* (Cresson, 1920)

General Distribution: AB, BC, NF, CO, NY, OH, PA, SD, WY.

Ohio Records (Figure 18C): **Champaign**, Cedar Swamp, X-08-1963, J. L. Williams, 1♂ (OSU); **Portage**, Kent, adult emerged from puparium, X-21-1965, B. A. Foote, 1♀ (CIMNH); 1.0 mile N Kent, III-27-1962, B. A. Foote, 1♂ reared from puparium (CMNH); 5.5 miles E Kent, IX-20-1965, B. A. Foote, 11 (gender not recorded) (CMNH); Mogadore Reservoir, IV-19-1962, B. A. Foote, 1♂ reared from puparium (CMNH).

Habitat: Marshes, fens, swamps.

Phenology: Multivoltine. Flight period in Ohio from early June to early October. Overwinters as pupa in floating or stranded host snail shell.

Biology: Larvae parasitoid on stranded pulmonate aquatic snails.

Immature Stages: None described.

16. *Pteromicra similis* Steyskal, 1954b

General Distribution: PQ; CT, MI, NJ, NY, OH.

Ohio Records (Figure 18D): **Portage**, 1.0 mile N Kent, III-20-1962, B. A. Foote, 13 reared from puparia in shells of *Planorbula jenkinsii* (CMNH); Streetsboro Bog, III-27-1962, B. A. Foote, 9 reared from puparia in shells of *P. jenkinsii* (CMNH); Mogadore Reservoir, IV-17-1962, B. A. Foote, 15 reared from puparia in shells of *P. jenkinsii* (CMNH); 7.0 miles E Kent, V-07-1962, B. A. Foote, 10 reared from puparia in shells of *P. jenkinsii* (CMNH); 6 miles SE Kent, IX-10-1965, B. A. Foote, 2♂, 1♀ (CMNH); 4.5 miles E Kent, III-16-1966, B. A. Foote, 12 reared from puparia in shells of *P. jenkinsii* (CMNH).

Habitat: Marshes, fens, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from early May to mid-September. Overwinters as pupa within shell of host snail.

Biology: Larva parasitoid of stranded aquatic snail belonging to *P. jenkinsii*.

Immature Stages: None described.

17. *Pteromicra spheura* Steyskal, 1954b

General Distribution: AZ, DC, MI, OH, SD.

Ohio Records (Figure 18E): **Lake**, Mentor Marsh, IX-25-1969, B. A. Foote, 4♂ (CMNH); **Portage**, 1.0 mile N Kent, III-20-1962, B. A. Foote, 7♂ reared from floating puparia (CMNH); Streetsboro Bog, III-27-1962, B. A. Foote, 2♂, 2♀ reared from floating puparia, Dollar Lake near Twin Lakes, VI-20-1962, D. Miletich, 1♂ (CMNH); 6 miles E Kent, X-01-1965, B. A. Foote, 1♀ (CIMNH); 6 miles SE Kent, IX-10-1965, B. A. Foote, 2♂, 1♀ (CMNH); Brady Lake, IV-26-1968, B. A. Foote, 1♂ reared from floating puparium (CMNH).

Habitat: Marshes, woodland pools.

Phenology: Multivoltine. Flight period in Ohio occurs from early June to mid-September. Overwinters as pupa within floating puparium.

Biology: Larva parasitoid/predator on stranded aquatic snails of the genera *Physa* and *Physella*.

Immature Stages: None described.

18. *Sciomyza aristalis* (Coquillett, 1901)

General Distribution: ONT, PQ; ME west to MI and OH.

Ohio Records (Figure 18F): **Portage**, 7 miles E Kent, VI-28-1963, E. J. Allen, 1♂ (CMNH).

Habitat: Marshes, floodplain forests.

Phenology: Trivoltine. Recorded in late June in Ohio. Overwinters as pupa in shell of host snail.

Biology: Larva parasitoid on land snails belonging to the genus *Succinea*. Egg deposited on shell of host snail (Foote, 1959).

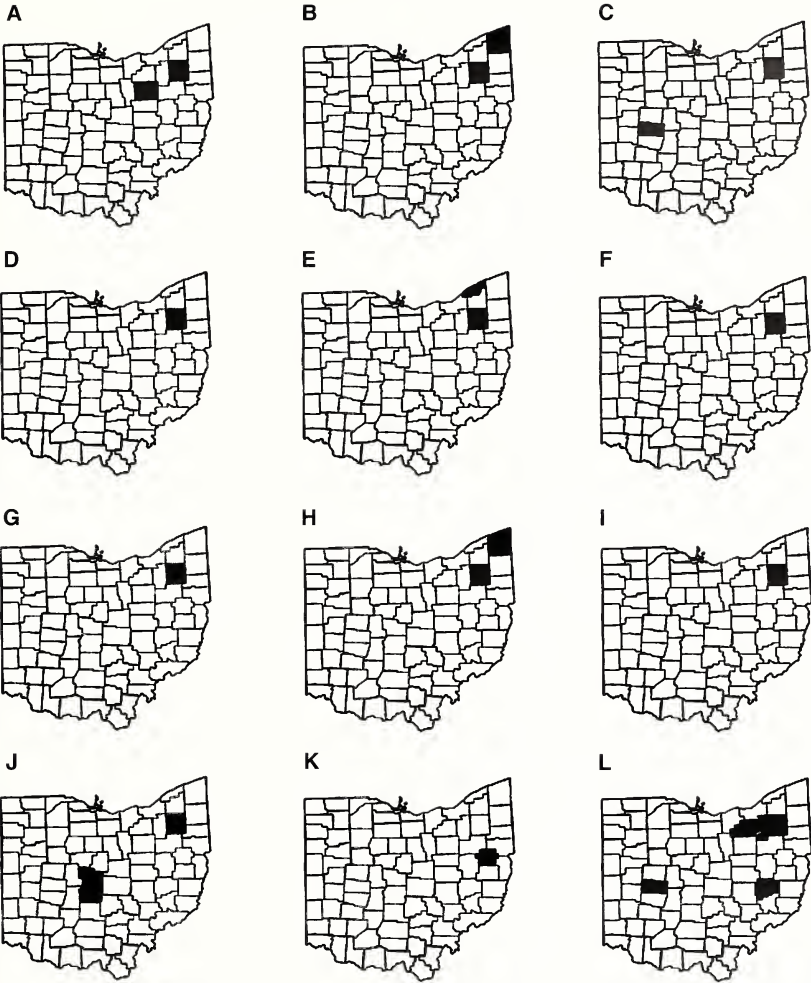


Figure 18. Distribution of Ohio Sciomyzidae. A, *Pherbellia similis*; B, *Pherbellia vitalis*; C, *Pteromicra pleuralis*; D, *Pteromicra similis*; E *Pteromicra sphenura*; F, *Sciomyza aristalis*; G, *Sciomyza varia*; H, *Antichaeta borealis*; I, *Antichaeta fulva*; J, *Antichaeta melanosoma*; K, *Dictya atlantica*; L, *Dictya borealis*.

Immature Stages: E, L₃, P (Foote, 1959).

19. *Sciomyza varia* (Coquillett, 1904)

General Distribution: AB, ONT, PQ; CA, CT, MI, MN, MT, NY, OH, SD, UT.

Ohio Records (Figure 18G): **Portage**, 5.0 miles S Kent, IV-24-1962, B. A. Foote, 2♂ reared from puparia in shells of *Stagnicola* sp. (CMNH); 3.0 miles E Ravenna, V-01-1968, B. A. Foote, 1♂ reared from shell in floating shell of *Stagnicola* sp. (CMNH).

Habitat: Marshes, swamps, woodland pools.

Phenology: Uni- or bivoltine. Recorded in Ohio only during late April and early May. Overwinters as pupa within the shell of host snail.

Biology: Larva parasitoid on aquatic snails belonging to the genus *Stagnicola*. Egg deposited on shell of host snail (Barnes, 1990).

Immature Stages: E, L₁₋₃, P (Barnes, 1990).

20. *Antichaeta borealis* Foote, 1961a

General Distribution: CA, IA, ID, MT, OH.

Ohio Records (Figure 18H): **Ashtabula**, Pymatuning Reservoir near Linesville, V-25-1963, B. A. Foote, 2♂ (CMNH); **Portage**, Mogadore Reservoir, IV-17-1962, B. A. Foote, 2♂ reared from floating puparia (CMNH); 4.5 miles E Kent, IV-20-1964, B. A. Foote, 1♂ reared from floating puparium (CMNH); 4.5 miles E Kent, V-10-1968, B. A. Foote, 2♂, 2♀ reared from floating puparia (CMNH); Kent, IV-06-1965, W. Robinson, 1♂ reared from floating puparium (CMNH).

Habitat: Marshes.

Phenology: Univoltine. Flight period in Ohio occurs in late May. Overwinters as pupa.

Biology: Larvae prey on eggs of terrestrial pulmonate snails belonging to the genera *Catinella* and *Oxyloma*. Eggs deposited on egg masses of host snails (Robinson and Foote, 1978).

Immature Stages: None described.

21. *Antichaeta fulva* Steyskal, 1960

General Distribution: AB; ID, NY, OH.

Ohio Records (Figure 18I): **Portage**, 1.0 mile E Kent, V-23-1967, B. A. Foote, 1♀ reared from floating puparium (CMNH); 4.5 miles E Kent, VI-01-1968, B. A. Foote, 1♂ reared from floating puparium (CMNH); 3.0 miles E Ravenna, V-01-1968, B. A. Foote, 1♂ reared from floating puparium.

Habitat: Marshes.

Phenology: Univoltine. Flight period in Ohio occurs in May. Overwinters as pupa in leaf litter.

Biology: Larvae prey on exposed eggs of aquatic pulmonate snails belonging to the genus *Lymnaea*. Eggs laid on egg masses of host snail.

Immature Stages: None described.

22. *Antichaeta melanosoma* Melander, 1920

General Distribution: Transcontinental in North America.

Ohio Records (Figure 18J): **Delaware**, Delaware, VI-10-1961, B. A. Foote, 1♂ (CMNH); **Franklin**, Columbus, V-09-1899, 1♂ (OSU); **Portage**, Kent, V-23-1967, K. Valley, 2♂ (CMNH); 1.4 miles E Kent, IV-11-1967, B. A. Foote, 1♀ reared from puparium (CMNH); 3.0 miles E Kent, V-23-1967, B. A. Foote, 1♂ reared from puparium (CMNH); 4.5 miles E Kent, VI-01-1968, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, swamps, vernal woodland pools.

Phenology: Univoltine. Flight period in Ohio occurs from late May to mid-June. Overwinters as pupa in leaf litter.

Biology: Larvae prey on exposed eggs of the pulmonate aquatic snails *Aplexa hypnorum* (L.) and *Physa* sp. Egg laid on egg mass of host snail (Knutson and Abercrombie, 1977).

Immature Stages: None described.

23. *Dictya atlantica* Steyskal, 1954c

General Distribution: Nearctic. ONT, PQ; IL, MO, NC, NY, OH, PA, VA.

Ohio Records (Figure 18K): **Carroll**, Specht Marsh, VI-21-1964, 1♂, E. J. Allen (CMNH).

Habitat: Marshes.

Phenology: Multivoltine. Flight period in Ohio is in late June. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

24. *Dictya borealis* Curran, 1932

General Distribution: Nearctic. AB, MB, ONT; GA, IL, MI, ND, NY, OH, PA, TX, WA, WI.

Ohio Records (Figure 18L): **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); **Guernsey**, 11.0 miles S Cambridge, VII-31-1969, E. J. Allen, 3♂ (CMNH); **Medina**, Lodi, VI-26-1916, 1♂ (OSU); **Portage**, 7 miles E Kent, V-16-1962, B. A. Foote, 3♂ (CMNH); **Summit**, Akron, VI-1927, J. S. Hine, 1♂ (OSU).

Habitat: Marshes.

Phenology: Multivoltine. Flight period occurs in Ohio from mid-June to late July. Overwinters as pupa in floating puparium.

Biology: Unknown.

Immature Stages: None described.

25. *Dictya expansa* Steyskal, 1938

General Distribution: Nearctic. Nearly transcontinental, south to FL and AZ.

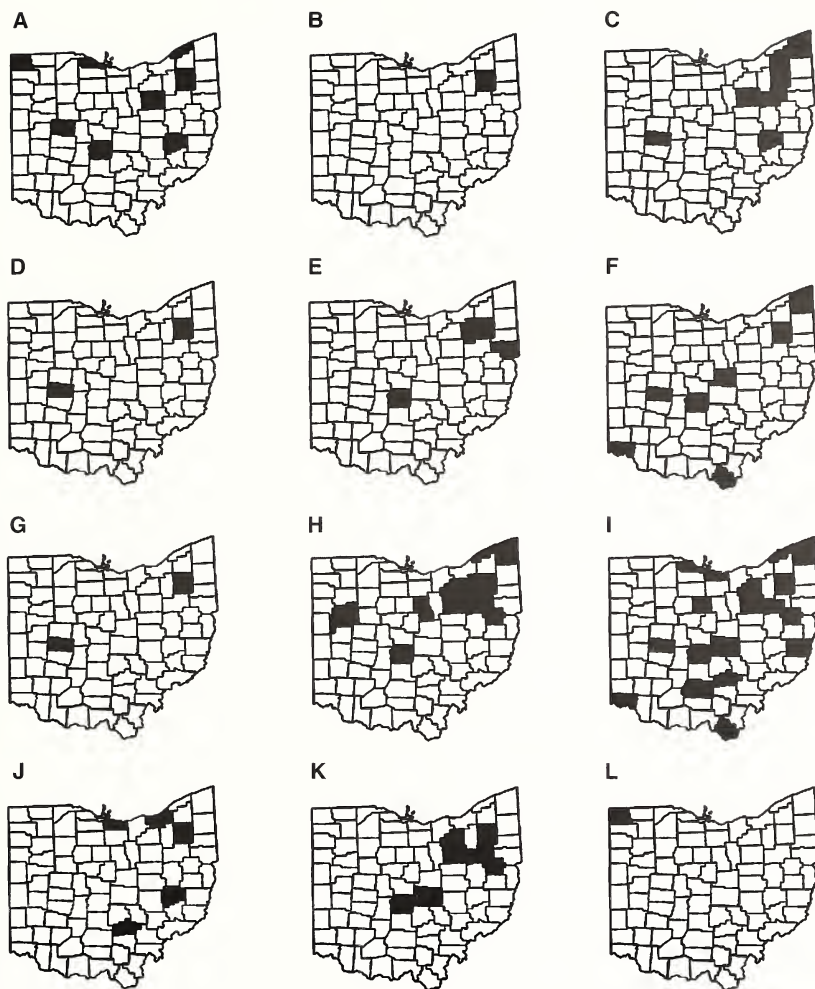


Figure 19. Distribution of Ohio Sciomyzidae. A, *Dictya expansa*; B, *Dictya hudsonica*; C, *Dictya pictipes*; D, *Dictya sabroskyi*; E, *Dictya steyskali*; F, *Dictya stricta*; G, *Dictya texensis*; H, *Elgiva sollicita*; I, *Euthycera arcuata*; J, *Limmia bosicii*; K, *Limmia conica*; L, *Limmia fitchi*.

Ohio Records (Figure 19A): **Champaign**, Cedar Swamp, VII-24-1964, J. L. Williams, 2♂ (OSU); **Franklin**, Columbus, IV-13-1899, 1♂ (OSU); **Guernsey**, 11.0 miles S. Cambridge, E. J. Allen, 1♂ (CMNH); **Lake**, Mentor Marsh, VI-08-1981, A. D. Huryn, 1♂ (CMNH); **Ottawa**, Gypsum, V-16-1912, F. L. King, 1♂ (OSU); **Portage**, 1.0 mile E Kent, V-14-1962, B. A. Foote, 4♂, 1♀ (CMNH); 7.0 miles E Kent, V-07-1962, B. A. Foote, 1♂ (CMNH); 1.0 mile N Kent, VI-01-1963, B. A. Foote, 1♂ (CMNH); 5.0 miles NW Kent, VI-25-1963, B. A. Foote, 1♂ (CMNH); Dollar Lake near Twin Lakes, VI-20-1962, D. Miletich, 1♂ (CMNH); **Wayne**, Wooster, IV-16-1898, 2♂ (OSU); Moreland, V-17-1959, C. A. Triplehorn, 1♂ (OSU); **Williams**, Mud Lake Bog State Nature Preserve, VI-03-07-2001, J. B. Keiper, 1♂ (CIMNH).

Habitat: Marshes, roadside ditches, marshy borders of lakes, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-April to late July. Overwinters as pupa within floating puparium.

Biology: Predacious on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

26. *Dictya hudsonica* Steyskal, 1954c

General Distribution: BC, PQ, CT, DE, IA, ID, IL, MI, MN, MT, NJ, NY, OH, WI, WY.

Ohio Records (Figure 19B): **Portage**, 2.0 miles E Kent, VII-05-1962, B. A. Foote, 1♂ (CMNH); Streetsboro Bog, IV-11-1963, B. A. Foote, 1♂ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-April to late September. Overwinters as pupa in floating puparium.

Biology: Predacious on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

27. *Dictya pictipes* (Loew, 1859)

General Distribution: ONT to MB, south to NC and AL.

Ohio Records (Figure 19C): **Ashtabula**, near Ashtabula/Geauga border at Route 322, VI-07-2002, J. B. Keiper, 2♂ (CIMNH); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); **Geauga**, Koeliker Fen, VIII-16-2001, J. B. Keiper, 1♂ (CIMNH); **Guernsey**, 11.0 miles S Cambridge, IV-04-1965, E. J. Allen, 1♂ (CMNH); **Portage**, 4.5 miles E Kent, IX-29-1968, R. Mangan, 1♂ (CMNH); 5.0 miles NW Kent, VI-25-1963, B. A. Foote, 1♂ (CMNH); Jennings Woods northeast of Ravenna, IV-23-1975, B. A. Foote, 1♂ (CMNH); Ravenna Arsenal, VIII-20-1996, J. B.

Keiper, 1♂ (CMNH); **Stark**, 3.0 miles NE Canton, V-30-1965, K. Valley, 1♂ (CMNH); **Wayne**, 0.5 miles S Rittman, VII-04-1970, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, swamps.

Phenology: Multivoltine. Flight period in Ohio from early April to late September. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

28. *Dictya sabroskyi* Steyskal, 1938

General Distribution: OH west to NE, south to FL and MEX.

Ohio Records (Figure 19D): **Champaign**, Cedar Swamp, V-21-1964, B. A. Foote, 1♂ (CMNH); **Portage**, Kent State campus, VII-10-1995, J. B. Keiper, 1♂ (CMNH).

Habitat: Fens, marshes.

Phenology: Multivoltine. Collected in Ohio from late May to mid-July. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

29. *Dictya steyskali* Valley, 1977 (in Valley and Berg, 1977)

General Distribution: NF, NS, ONT; MA, ME, MI, NY, OH, PA, VT.

Ohio Records (Figure 19E): **Columbiana**, Beaver Creek State Park, VII-03-2000, B. A. Foote, 1♂ (CMNH); **Fayette**, Deer Creek State Park, VI-08-1997, J. B. Keiper, 1♂ (CMNH); **Portage**, Herrick Fen, VIII-21-1989, B. A. Foote, 1♂ (CMNH); **Horning Road Marsh** in east Kent, VI-02-1989, B. A. Foote, 1♂ (CMNH); **Summit**, Singer Lake Bog, VII-10-2002, J. B. Keiper, 3♂ (CIMNH).

Habitat: Marshes, fens.

Phenology: Multivoltine. Flight period in Ohio occurs from early June to late August. Overwinters as pupa.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

30. *Dictya stricta* Steyskal, 1938

General Distribution: BC; AL, CO, KS, KY, IL, LA, MS, MT, NC, NE, OH, TX.

Ohio Records (Figure 19F): **Ashtabula**, Pymatuning Creek Fen, VI-21-2001, J. B. Keiper, 1♂ (CIMNH); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); Cedar Swamp, V-27-1961, R. E. Woodruff, 1♂ (FSCA); **Franklin**, Columbus, V-15-1902, J. S. Hine, 1♂ (OSU); **Hamilton**, Cincinnati, VI-26-1974, W. Downing, 1♂ (CMNH); **Knox**, Danville, V-19-1899, 1♂ (OSU); **Lawrence**, Ironton, V-1926, 1♂ (OSU); **Portage**, 1 mile N

Kent, VI-01-1963, B. A. Foote, 1♂ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, fens, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-May to late September. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

31. *Dictya texensis* Curran, 1932

General Distribution: PA to WY, south to FL and CA and MEX.

Ohio Records (Figure 19G): **Champaign**, Cedar Swamp, VII-12-1962, R. E. Woodruff, 2♂ (FSCA); Cedar Swamp, VII, VIII-1964, J. L. Williams, 24♂ (OSU); **Portage**, 4.5 miles E Kent, III-30-1964, 6♂ reared from floating puparia (CMNH); 5.0 miles E Kent, V-20-1964, B. A. Foote, 1♂ reared from floating puparium (CMNH); Dollar Lake near Twin Lakes, IV-21-1963, B. A. Foote, 2♂ reared from floating puparia (CMNH).

Habitat: Marshes, fens, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from early April to late August. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Valley and Berg, 1977).

Immature Stages: E, L₁₋₃, P (Valley and Berg, 1977).

32. *Elgiva sollicita* (Harris, 1780)

General Distribution: Nearctic. AK to NF, south to VA and CA.

Ohio Records (Figure 19H): **Allen**, Spencerville, VII-18-2001, J. B. Keiper, 2♂ (CIMNH); **Ashtabula**, Pymatuning Creek Fen, VI-21-2001, J. B. Keiper, 1♂, 8♀ (CIMNH); **Auglaize**, Grand Lake St. Marys State Park, VII-18-2001, J. B. Keiper, 2♂, 1♀ (CIMNH); **Carroll**, Specht Marsh, VII-27-1963, E. J. Allen, 3♂ (CMNH); **Franklin**, Columbus, VI-16-1963, A. Peterson, 1♀ (OSU); **Lake**, Mentor Marsh, VI-08-1981, A. D. Huryn, 5♂, 3♀ (CMNH); **Medina**, 2.0 miles N. Wadsworth, E. J. Allen, 1♀ (CMNH); **Portage**, 5.0 miles S Kent, VI-22-1964, E. J. Allen, 2♂ (CMNH); 8.0 miles S Kent, VII-22-1964, E. J. Allen, 2♂, 4.0 miles E Kent, VI-29-1965, K. Valley, 1♂ (CMNH); 6.0 miles SE Kent, IX-02-1965, K. Valley, 1♂ (CMNH); Dollar Lake near Twin Lakes, VIII-09-1962, D. Miletich, 1♀ (CMNH); Herrick Fen, 3 miles NW Kent, VI-16-1969, B. A. Foote, 1♂ (BAF); Jay Lake, VII-02-1965, D. Miletich, 1♂ (CMNH); Streetsboro Bog, VIII-05-1964, R. C. McConnell, 1♀ (CMNH); West Branch State Park, VII-31-1997, J. B. Keiper,

2♂ (CMNH); **Richland**, Mansfield, swamp near Route 30/71, VII-18-2001, J. B. Keiper, 1♂, 6♀; **Stark**, KSU Stark campus, III-12-1995, E. G. Chapman, 1♂ (CMNH); wetlands near Route 30/Trump Road junction, VI-20-2001, J. B. Keiper, 1♂ (CIMNH); **Summit**, Akron, VI-1923, J. S. Hine, 1♂ (OSU); Ira, J. S. Hine, 1♂ (OSU); **Wayne**, Moreland, V-17-1959, C. A. Triplehorn, 10♂ (OSU); Rittman, VII-12-1964, W. B. Stoltzfus, 1♂ (CMNH).

Habitat: Marshes, fens, swamps, roadside ditches.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-May to late September. Overwinters as adult.

Biology: Larvae prey on pulmonate aquatic snails (Knutson and Berg, 1964).

Immature Stages: E, L₁₋₃, P (Knutson and Berg, 1964).

33. *Euthycera arcuata* (Loew, 1859)

General Distribution: ON to WY, south to GA, LA, and TX.

Ohio Records (Figure 19I): **Ashtabula**, North Kingsville Sand Barrens, VI-12-2001, B. A. Foote, 1♂ (CIMNH); **Belmont**, Bethesda, V-25-1974, B. A. Foote, 1♂ (CMNH); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 3♂, 3♀ (CMNH); Cedar Swamp, VII-11-1964, J. L. Williams, 1♂ (OSU); **Carroll**, Specht Marsh, VII-27-1964, E. J. Allen, 1♀; **Columbiana**, Beaver Creek State Park, VI-16-1996, J. B. Keiper, 1♀ (CMNH); **Crawford**, Galion, VI, 1♀ (OSU); **Erie**, Sandusky, VI-30-1900, J. S. Hine, 1♀ (OSU); **Fayette**, Deer Creek State Park, VI-08-1997, J. B. Keiper, 1♂ (CIMNH); **Hamilton**, Cincinnati, VI-09, 21-1974, W. Downing, 2♀ (CMNH); **Hocking**, Cantwell Cliffs, VI-07-1941, R. C. Osburn, 1♂ (OSU); **Lawrence**, Ironton, V-26-1899, J. S., Hine, 1♀ (OSU); **Licking**, Newark, VI-21, D. J. and J. N. Knull, 1♀ (OSU); **Medina**, Medina, VI-10-1899, J. S. Hine, 1♀ (CMNH); 2.0 miles N Wadsworth, VI-30-1964, E. J. Allen, 1♂ (CMNH); **Ottawa**, Gypsum, VII-12-1912, F. L. King, 1♂, 1♀ (OSU); **Portage**, 4.0 miles E Kent, VI-15-1963, B. A. Foote, 1♂ (CMNH); 11.0 miles W Kent, VII-04-1967, G. Piper, 2♀ (CMNH); Streetsboro Bog, VII-08-1964, E. J. Allen, 3♀ (CMNH); **Ross**, no locality given, VII-01-1943, D. J. Borror, 1♂ (OSU); **Wayne**, 1.0 mile E Rittman, VII-19-1964, W. B. Stoltzfus, 1♀ (CMNH).

Habitat: Woodland swamps, beech-maple forests, oak-hickory forests, mixed mesophytic forests, marshes.

Phenology: Univoltine. Flight period in Ohio occurs from late May to late September. Overwinters as larva within partially eaten land snails.

Biology: Poorly known. Nearly mature larvae have been found feeding within the land snails *Mesodon inflectus* (Say), *Stenotrema hirsutum* (Say), and *Ventridens lig-*

era (Say), but no complete life cycle is available.

Immature Stages: None described.

34. *Limnia boscii* (Robineau-Desvoidy, 1830)

General Distribution: Nearctic; ON and ME to MT, south to VA, IA, and NE.

Ohio Records (Figure 19J): **Cuyahoga**, Chagrin River, VI-22-2002, J. B. Keiper, 1♀ (CIMNH); **Erie**, Shimrock, V-23-1986, S. M. Clark, 2♂ (CMNH); **Guernsey**, Cambridge, IV-04-1965, R. E. MacConnell, 1♂ (CMNH); **Hocking**, near Conkles Hollow State Park, VII-14-1997, J. B. Keiper, 1♀ (CMNH); **Portage**, KSU campus, VII-10-1995, J. B. Keiper, 1♂ (CIMNH), 4.5 miles E Kent, VII-30-1961, D. Miletich, 1♂ (CMNH); 2 miles NE Kent, VI-12-1995, B. A. Foote, 1♂ (CIMNH).

Habitat: Marshes.

Phenology: Voltinism unknown.

Biology: Overwintered third-instar attacks a variety of pulmonate aquatic snails, but the food of newly hatched larva remains unknown.

Immature Stages: None described.

35. *Limnia conica* Steyskal, 1978 (in Steyskal et al., 1978)

General Distribution: Nearctic; NB to ON and MN, south to VA, AL, and AR.

Ohio Records (Figure 19K): **Carroll**, Specht Marsh, no further data given; **Franklin**, Columbus, Blacklick Woods; **Licking**, no date or locality data (Steyskal et al., 1978); **Medina**, 3 miles W Wadsworth; **Portage**, 1.0 mile E Kent, IX-10-1997, B. A. Foote, 3♂, 2♀ (CMNH); **Towners Woods**, VI-15-1999, B. A. Foote, 5♂, 4♀ (CMNH); **Stark**, 3 miles NE Canton; **Wayne**, 1 mile E Rittman (Steyskal et al., 1978).

Habitat: Old fields, borders of marshes and fens.

Phenology: Voltinism unknown. Flight period in Ohio occurs from mid-June to mid-September.

Biology: Unknown.

Immature Stages: None described.

36. *Limnia fitchi* Steyskal, 1978 (in Steyskal et al., 1978)

General Distribution: Nearctic; NF to BC, south to NJ, LA, and NM.

Ohio Records (Figure 19L): **Williams**, Mud Lake Bog State Nature Preserve, VI-03-07-2001, J. B. Keiper, 2♂ (CIMNH).

Habitat: Marshes.

Phenology: Voltinism unknown. Only one Ohio record from a malaise trap series. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

37. *Limnia georgiae* Melander, 1920

General Distribution: Nearctic; AL, GA, IL, KS, MI, NC, NJ,

NY, NC, OH, TN, VA, WV.

Ohio Records (Figure 20A): **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH).

Habitat: Fens.

Phenology: Voltinism unknown. Only recorded from Ohio in mid-June. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

38. *Limnia loewi* Steyskal, 1965

General Distribution: Nearctic; NS to ON, south to GA and AL.

Ohio Records (Figure 20B): **Portage**, Jennings Woods, VII-24-1998, J. B. Keiper, 5♀ (CMNH); Jennings Woods, VIII-10-1994, B. A. Foote, 1♂ (CMNH); 6.0 miles E Kent, IX-02-1967, B. A. Foote, 1♂ (CMNH).

Habitat: Floodplain woods, swamps.

Phenology: Voltinism unknown. Flight period in Ohio occurs from late July to early September. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

39. *Limnia nanbai* Steyskal, 1978 (in Steyskal et al., 1978)

General Distribution: Nearctic; CT, GA, IA, IL, MI, NC, OH, VA, WI (Steyskal et al., 1978).

Ohio Records (Figure 20C): **Franklin**, Columbus, V-18-1899, J. S. Hine, 1♂ (OSU); **Fairfield**, Lancaster, VII-04-1930, J. S. Hine, 1♂, (USNM); **Lucas**, VII-1911, R. C. Osburn, 1♂ (OSU).

Habitat: Unknown.

Phenology: Voltinism unknown. Flight period in Ohio occurs from mid-May to early July. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

40. *Limnia ottawensis* Melander, 1920

General Distribution: NB to AB, south to AL and CA.

Ohio Records (Figure 20D): **Franklin**, Columbus, VII-27-1920, 1♂, no collector recorded (ILNHS).

Habitat: Marshes.

Phenology: Voltinism unknown. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

41. *Limnia saudovalensis* Fisher and Orth, 1978 (in Steyskal et al., 1978)

General Distribution: Nearctic; NF to AK, south to DC and NM (Knutson et al., 1986).

Ohio Records (Figure 20E): **Portage**, Streetsboro Bog, no further data given (Steyskal, 1978).

Habitat: marshes, fens.

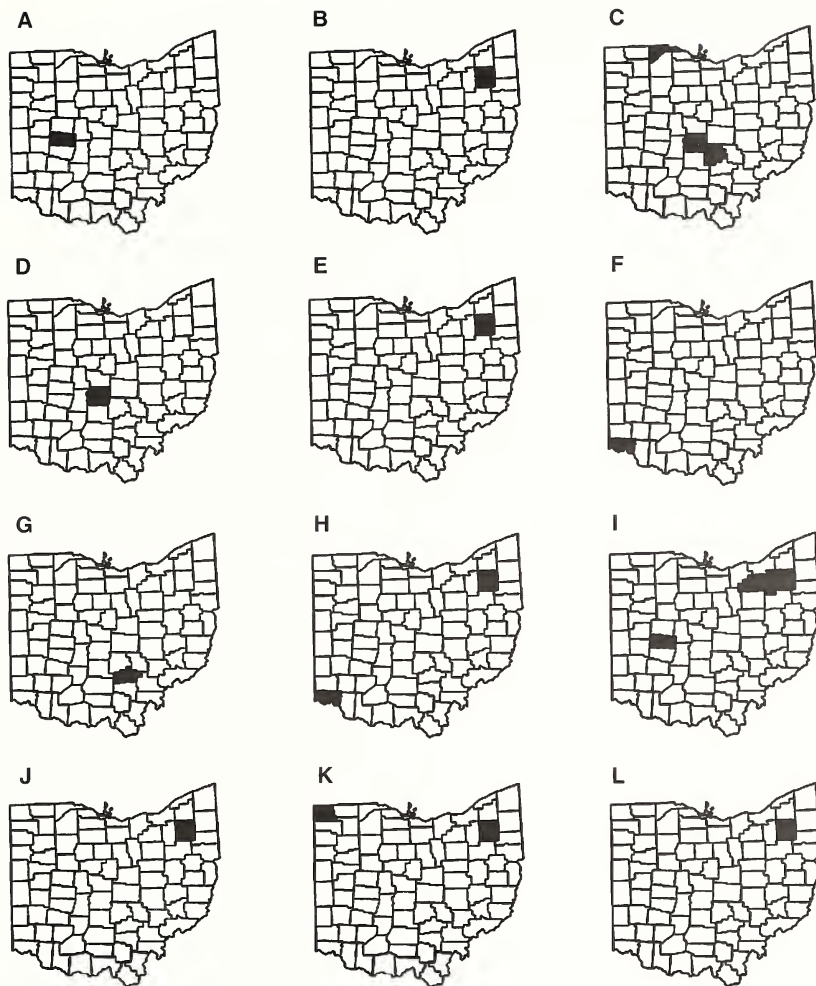


Figure 20. Distribution of Ohio Sciomyzidae. A, *Limnia georgiae*; B, *Limnia loewi*; C, *Limnia nambai*; D, *Limnia ottawensis*; E, *Limnia sandovalensis*; F, *Limnia septentrionalis*; G, *Limnia shamoni*; H, *Limnia sparsa*; I, *Poecilographa decora*; J, *Renocera amanda*; K, *Renocera brevis*; L, *Renocera longipes*.

Phenology: Voltinism unknown. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

42. *Limnia septentrionalis* Melander, 1920

General Distribution: Nearctic; AL, AR, DC, IL, MD, NJ, NC, OH, PA, TN, VA.

Ohio Records (Figure 20F): **Hamilton**, Cincinnati, VI-29-1974, W. Downing, 1♂ (CMNH).

Habitat: Unknown.

Phenology: Voltinism unknown. Recorded from Ohio only in late June. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

43. *Limnia shannoni* Cresson, 1920

General Distribution: Nearctic; AL, AR, FL, GA, LA, MD, NJ, OH, TN (Steyskal et al., 1978).

Ohio Records (Figure 20G): **Hocking**, X-16-1941, D. J. and J. N. Knull, 1♂ (OSU).

Habitat: Unknown.

Phenology: Voltinism unknown. Recorded in Ohio only in mid-October. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

44. *Limnia sparsa* (Loew, 1862)

General Distribution: Nearctic. NF to BC, south to NC and OH.

Ohio Records (Figure 20H): **Hamilton**, Cincinnati, VI-02-1974, W. Downing, 1♂ (CMNH); **Portage**, J. Arthur Herrick State Nature Preserve, VII-10-1986, 2♂, B. A. Foote (CMNH).

Habitat: Marshes.

Phenology: Voltinism unknown. Recorded from Ohio only in early July. Overwintering habits unknown.

Biology: Unknown.

Immature Stages: None described.

45. *Poecilographa decora* (Loew, 1864)

General Distribution: Nearctic: NB to SK, south to VA, LA, and CO.

Ohio Records (Figure 20I): **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); **Medina**, Medina, VII-11-1898, J. S. Hine, 1♂ (OSU); **Portage**, 4.5 miles E Kent, VII-30, VIII-14-1962, D. Trelka, 5♂ (CMNH); 7.0 miles E Kent, VI-28, VII-09-1963, B. A. Foote, 2♀ (CMNH).

Habitat: Marshes, fens, swamps.

Phenology: Probably univoltine. Flight period in Ohio occurs from mid-June to mid-August. Overwinters as pupa (Barnes, 1988).

Biology: Largely unknown. Newly hatched larvae did not attack a wide variety of Mollusca in laboratory

rearings (Barnes, 1988).

Immature Stages: L₃, P (Barnes, 1988).

46. *Renocera amanda* Cresson, 1920

General Distribution: Nearctic. BC, NB, ONT, PQ; IN, ME, MN, NC, NY, OH, PA, SD.

Ohio Records (Figure 20J): **Portage**, Towners Woods, VI-01-1965, B. A. Foote, 1♂ (CMNH); 1.0 mile N Kent, V-14-1962, B. A. Foote, 4♂, 3♀ (CMNH); 4.0 miles N Kent, V-16-1962, B. A. Foote, 2♂ (CMNH); 4.5 miles E Kent, VI-28-1965, K. Valley, 1♂ (CMNH); Kent, V-23-1967, K. Valley, 2♂ (CMNH); Jennings Woods, V-07-1962, B. A. Foote, 1♀ (CMNH).

Habitat: Swamps, woodland vernal pools.

Phenology: Univoltine. Flight period in Ohio occurs from early May to mid-July. Overwinters as pupa in leaf litter or floating debris.

Biology: Larvae prey on fingernail clams (Sphaeriidae) (Foote, 1976).

Immature Stages: None described.

47. *Renocera brevis* Cresson, 1920

General Distribution: Nearctic. AB, NF, ONT, YUK; AK, CA, CO, MT, NM, NY, OH, WA.

Ohio Records (Figure 20K): **Portage**, Kent, VI-19-1965, B. A. Foote, 1♂ (CMNH); 4.5 miles E Kent, III-30-1964, E. J. Allen, 3♂, 2♀ emerged from floating puparia (CMNH); VI-29-1964, E. J. Allen, 1♂ (CMNH); VII-23-1965, W. H. Robinson, 3♂ (CMNH); Dollar Lake near Twin Lakes, VI-20-1962, D. Miletich, 1♂ (CMNH); **Williams**, Mud Lake Bog State Nature Preserve, VI-03-07-2001, J. B. Keiper, 1♂ (CMNH).

Habitat: Marshes, marshy borders of lakes and ponds.

Phenology: Bi- or trivoltine. Flight period in Ohio occurs from early May to late July. Overwinters as pupa floating in shallow water or in shoreline litter.

Biology: Larvae prey on fingernail clams of the genera *Musculium*, *Psidium*, and *Sphaerium* (Sphaeriidae) (Foote and Knutson, 1970; Foote 1976).

Immature Stages: None described.

48. *Renocera longipes* (Loew, 1876)

General Distribution: Nearctic. NB, NF, ONT, PQ; CT, MA, NH, OH, PA, WV.

Ohio Records (Figure 20L): **Portage**, 4.0 miles N Kent, VI-15-1963, B. A. Foote, 2♂ (CMNH); 4.5 miles E Kent, VI-18-1965, W. H. Robinson, 1♂ (CMNH); VI-23-1965, K. Valley, 2♂ (CMNH); 7.0 miles E Kent, VI-24-1963, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, swamps.

Phenology: Univoltine. Flight period in Ohio occurs from late May to late June. Overwinters as pupa.

Biology: Larvae prey on fingernail clams (Foote, 1976).

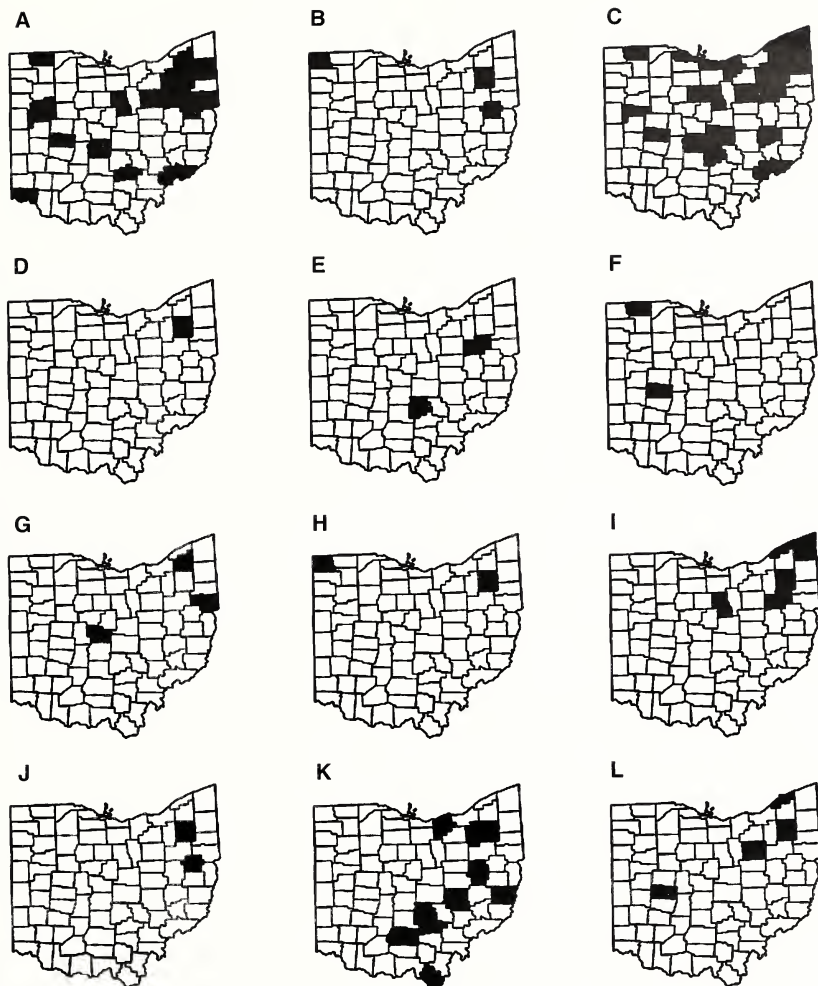


Figure 21. Distribution of Ohio Sciomyzidae. A, *Sepedon armipes*; B, *Sepedon borealis*; C, *Sepedon fuscipennis*; D, *Sepedon gracilicornis*; E, *Sepedon lignator*; F, *Sepedon neili*; G, *Sepedon pusilla*; H, *Sepedon spinipes americana*; I, *Sepedon tenuicornis*; J, *Tetanocera annae*; K, *Tetanocera clara*; L, *Tetanocera ferruginea*.

Immature Stages: None described.

49. *Sepedon arripes* Loew, 1859

General Distribution: Nearctic, Transcontinental, south to VA, OH, and northern Mexico (Knutson and Orth, 2001).

Ohio Records (Figure 21A): **Allen**, Spencerville, VII-18-2001, J. B. Keiper, 1♂ (CMNH); **Ashtabula**, Pymatuning Reservoir near Simmons, VII-10-1962, D. Miletich, 1♂ (CMNH); **Auglaize**, near Lima, VII-18-2001, J. B. Keiper, 3♂ (CMNH); **Carroll**, VII-27-1964, E. J. Allen, 2♂ (CMNH); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); VII-12-1962, R. E. Woodruff, 1♂ (FSCA); VI-X-1964, J. L. Williams, 29 (OSU); **Columbiana**, Beaver Creek State Park, VI-16-1996, J. B. Keiper, 1♂ (CMNH); **Franklin**, Columbus, IV-19-1941, R. C. Osburn, 1♂ (OSU), IV-21, V-05, V-10-1899, J. S. Hine, 3♂ (OSU); VI-16-1936, A. Peterson, 3♂ (OSU); **Fulton**, Wauseon, VIII-25-1902, J. S. Hine, 1♀ (OSU); **Geauga**, Koelliker Fen, VIII-16-2001, J. B. Keiper, 1♂ (CMNH); **Hamilton**, Cincinnati, VI, VIII-1974, W. Downing, 6♂, 7♀ (CMNH); **Hocking**, OSU Barneby Center, V-14-1983, 1♂ (OSU); Near Conkles Hollow State Park, VII-14-1998, 1♂ (OSU); **Portage**, 1.0 mile N Kent, V-14-1962, B. A. Foote, 1♂ (CMNH); 1.0 mile S Kent, VIII-07-1964, W. B. Stoltzfus, 1♂ (CMNH); 4.0 miles N Kent, X-04-1961, B. A. Foote, 1♂ (CMNH); 7.0 miles E Kent, V-07-1962, B. A. Foote, 1♂ (CMNH); 6.0 miles SE Kent, IX-02-1965, K. Valley, 1♂ (CMNH); Ravenna Arsenal, VII-12-1996, J. B. Keiper, 2♂ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 1♂ (CMNH); 3.0 miles E Streetsboro, VII-19-1998, B. A. Foote, 1♂ (CMNH); **Richland**, Mansfield, swamp near Route 30/71, VII-18-2001, J. B. Keiper, 1♂ (CMNH); 4.0 NE Plymouth, IX-08-65, J. A. Ferancak, 1♂ (CMNH); 4.0 miles W Plymouth, VIII-28-1965, K. Valley, 2♂ (CMNH); **Stark**, no locality given, VIII-18-1964, B. A. Foote, 1♂ (CMNH); **Summit**, Barberton, VIII-01-1996, J. B. Keiper, 1♂ (CMNH); alkaline area near Barberton, VIII-26-1997, J. B. Keiper, 1♂ (CMNH); **Washington**, Lake Veto Wildlife Area, VIII-05-1997, J. B. Keiper, 1♂ (CMNH); **Wayne**, Moreland, V-17-1959, V-17-1959, C. A. Triplehorn, 1♂, 1♀ (OSU).

Habitat: Marshes, marshy borders of ponds and lakes, drainage ditches, riparian areas.

Phenology: Multivoltine. Flight period in Ohio occurs throughout the year as adult overwinters.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

50. *Sepedon borealis* Steyskal, 1951

General Distribution: Transcontinental in Canada to AK, south to GA, west to CA (Knutson and Orth, 2001).

Ohio Records (Figure 21B): **Carroll**, Specht Marsh, VII-27-1964, E. J. Allen, 1♂ (CMNH); **Portage**, J. Arthur Herrick State Nature Preserve, VII-10-1986, B. A. Foote, 1♂ (CMNH); **Williams**, Mud Lake Bog State Nature Preserve, VI-03-07-2001, J. B. Keiper, 2♂ (CMNH).

Habitat: Marshes, marshy borders of ponds and lakes, drainage ditches.

Phenology: Multivoltine. Flight period in Ohio is throughout the year, as this species overwinters as an adult.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

51. *Sepedon fuscipectus* Loew, 1859

General Distribution: ON to AK, south to FL, TX, and WA (Knutson and Orth, 2001).

Ohio Records (Figure 21C): **Ashtabula**, Pymatuning Creek Fen, VI-18-2001, J. B. Keiper, 1♂, 1♀ (CMNH); Pymatuning Reservoir near Simmons, VII-10-1962, D. Miletich, 1♀ (CMNH); Route 322, western area of county, VI-21-2001, J. B. Keiper, 4♀, 1♂ (CMNH); **Auglaize**, Grand Lake St. Marys State Park, VII-18-2001, J. B. Keiper, 9♀ (CMNH); **Champaign**, Cedar Swamp, IX-25-1963, VII-11-1964, J. L. Williams, 1♂, 1♀ (OSU); **Crawford**, Galion, VII (OSU); **Erie**, Sandusky, VI-15-1899, J. S. Hine, 1♂ (OSU); **Franklin**, Columbus, J. S. Hine, 2♂ (OSU); **Fulton**, Wauseon, VIII-24-1902, J. S. Hine, 2♀ (OSU); **Geauga**, Cuyahoga River at Route 422, VII-14-1979, 1♀ (OSU); South Newbury, XI-18-1934, RFK, 1♀ (CMNH); **Guernsey**, 11.0 miles S Cambridge, VII-31-1964, E. J. Allen, 1♀ (CMNH); **Lake**, Mentor Marsh, VI-08-1981, V-30-1982, A. D. Huryn, 2♂, 3♀ (CMNH); **Licking**, Newark, VIII-27-1899, R. C. Osburn, 1♂ (OSU); **Lorain**, Oakpoint west of Lorain, VIII-12-1961, D. Deonier, 1♂ (IASU); **Portage**, KSU campus, VII-16-1995, J. B. Keiper, 1♂ (CMNH); 1.0 mile N Kent, V-14-1962, B. A. Foote, 1♀ (CMNH); 4.0 miles N Kent, V-16-1962, B. A. Foote, 1♂ (CMNH); 5.0 miles N Kent, V-25-1962, B. A. Foote, 3♂, 2♀ (CMNH); 6.0 miles SE Kent, IX-02-1962, K. Valley, 1♀ (CMNH); Wingfoot Lake, IX-08-1961, B. A. Foote, 1♂ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 2♂ (CMNH); West Branch State Park, X-20-1994, J. B. Keiper, 1♀ (CMNH); **Richland**, Mansfield, swamp near Route 30/71, VII-18-2001,

J. B. Keiper, 1♂, 11♀ (CIMNH); **Stark**, wetlands near Route 30/Trump Road junction, VI-20-2001, J. B. Keiper, 2♀; **Summit**, Akron, VI, J. S. Hine, 1♀ (OSU); **Hawkins**, VI-27-1902, J. S. Hine, 1♀ (OSU); **Sugar Grove**, V-17-1902, 1♂ (OSU); **Wayne**, Moreland, V-17-1959, C. A. Triplehorn, 3 (gender not recorded) (OSU).

Habitat: Marshes, fens, roadside ditches, swamps.

Phenology: Multivoltine. Flight period in Ohio is throughout the year as adults overwinter.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

52. *Sepedon gracilicornis* Orth, 1986

General Distribution: Nearctic. ON, PQ; CT, IA, ME, MI, MN, NY, OH, PA.

Ohio Records (Figure 21D): **Portage**, 1.0 mile N Kent, V-24-1962, B. A. Foote, 1♂ (CMNH); 5.0 miles SE Kent, VII-04-1965, W. H. Robinson, 1♂, 1♀ (CMNH); 4.5 miles E Kent, VII-20-1967, B. A. Foote, 1♂ (CMNH); **Dollar Lake** near Twin Lakes, VIII-09-1962, D. Miletich, 1♂ (CMNH).

Habitat: Marshes, shrubby swamps.

Phenology: Multivoltine. Flight period in Ohio occurs throughout the year as adults overwinter.

Biology: Unknown.

Immature Stages: None described.

53. *Sepedon ligatur* Steyskal, 1951

General Distribution: Nearctic. AB, BC, NF, ONT; MT, NY, OH, WY.

Ohio Records (Figure 21E): **Fairfield**, Sugar Grove, V-17-1902, 2♂ (OSU); **Stark**, Stewart Bog, VIII-16-1964, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, fens, bogs.

Phenology: Multivoltine. Flight period in Ohio is probably throughout the year as adults overwinter.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: None described.

54. *Sepedon neili* Steyskal, 1951

General Distribution: Nearctic. MB, PQ; GA, ID, MA, MI, MT, OH, UT.

Ohio Records (Figure 21F): **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 4 (CMNH); Cedar Swamp, VI-21-1964, B. A. Foote, 4♂ (CMNH); Cedar Swamp, VII-12-1962, R. E. Woodruff, 4♂ (FSCA); Cedar Swamp, VII-VIII-1964, R. L. Williams, 11♂ (OSU); **Fulton**, Wauseon, VIII-25-1902, J. S. Hine, 2♂ (OSU).

Habitat: Marshes, fens.

Phenology: Multivoltine. Flight period in Ohio is throughout

the year, as the adult overwinters.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

55. *Sepedon pusilla* Loew, 1859

General Distribution: Nearctic. DC, GA, IN, MS, OH.

Ohio Records (Figure 21G): **Delaware**, Delaware, IV-23-1955, B. A. Foote, 1♂ (CMNH); **Geauga**, Koelliker Fen, VIII-16-2001, J. B. Keiper, 1♂ (CIMNH); **Columbiana**, Beaver Creek State Park, VI-16-1996, J. B. Keiper, 3♂ (CIMNH).

Habitat: Marshes, fens.

Phenology: Multivoltine. Occurs throughout the year as adult overwinters.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

56. *Sepedon spinipes americana* Steyskal, 1951

General Distribution: Nearctic. NB to AK, south to OH, UT, and CA (Knutson and Orth, 2001).

Ohio Records (Figure 21H): **Portage**, 1.0 mile N Kent, V-24-1962, B. A. Foote, 1♀ (CMNH); 4.5 miles E Kent, VII-20-1967, D. Trelka, 1♂ (CMNH); **Dollar Lake** near Twin Lakes, VI-20-1962, D. Miletich, 1♂ (CMNH); **Dollar Lake** near Twin Lakes, VII-20-1967, D. Trelka, 1♂ (CMNH); **Williams**, Mud Lake Bog State Nature Preserve, VI-03-07-2001, J. B. Keiper, 1♂ (CIMNH).

Habitat: Marshes.

Phenology: Multivoltine. Occurs throughout the year as adults overwinter.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

57. *Sepedon tenuicornis* Cresson, 1920

General Distribution: Nearctic. ONT, PQ; ME, MN, MT, NE, OH, PA, SC, TX.

Ohio Records (Figure 21I): **Ashtabula**, Pymatuning Creek Fen, VI-18-2001, J. B. Keiper, 1♂, 8♀ (CIMNH); **Lake**, Mentor Marsh, VI-08-1961, B. A. Foote, 1♂ (CMNH); **Portage**, 1.0 mile N Kent, V-14-1962, B. A. Foote, 3♂ (CMNH); 4.0 miles E Kent, V-16-1962, B. A. Foote, 1♂ (CMNH); 5.0 miles S Kent, V-25-1962, 1♂ (CMNH); 5.0 miles SE Kent, VII-04-1965, W. H. Robinson, 2♂ (CMNH); **Streetsboro** Bog, VI-17-1964, E. J. Allen, 1♂ (CMNH); **Richland**, Mansfield, swamp near Route 30/71, J. B. Keiper, 2♂, 2♀ (CIMNH); **Stark**, Jackson Bog, IV-09-2001, R. Schriff, 1♂ (CIMNH).

Habitat: Marshes, fens.

Phenology: Multivoltine. Flight period in Ohio is throughout

year as adults overwinter.

Biology: Larvae prey on pulmonate aquatic snails (Neff and Berg, 1966).

Immature Stages: E, L₁₋₃, P (Neff and Berg, 1966).

58. *Tetanocera annae* Steyskal, 1938

General Distribution: ON to BC, south to CT, OH, and WI.

Ohio Records (Figure 21J): **Carroll**, Specht Marsh, VI-21, VII-27-1964, E. J. Allen, 1♂ 1♀ (CMNH); **Portage**, 4.5 miles E Kent, V-10, VI-01-1968, B. A. Foote, 2♂ (CMNH); 5.0 miles SE Kent, VI-23-1954, E. J. Allen, 1♂ (CMNH); 6.0 miles SE Kent, X-01-1965, B. A. Foote, 1♂ (CMNH); Mogadore Reservoir, IV-17-1992, B. A. Foote, 1♂, 1♀ reared from floating puparium (CMNH); Ravenna Arsenal, VIII-12-1996, J. B. Keiper, 1♂, 1♀ (CMNH); Streetsboro Bog, III-27-1962, B. A. Foote, 1♀ reared from floating puparium (CMNH).

Habitat: Buttonbush swamps, floodplain swamps.

Phenology: Univoltine. Flight period in Ohio is from early May to early October. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Foote, 1999).

Immature Stages: E, L₁₋₃, P (Foote, 1961b).

59. *Tetanocera clara* Loew, 1862

General Distribution: Nearctic. ON to PQ, south to GA, TN and IL.

Ohio Records (Figure 21K): **Belmont**, Bethesda, VI-15-1975, B. A. Foote, 2♀ (CMNH); **Fairfield**, no date/locality data given, 1♂ (OSU); **Hocking**, near Conkles Hollow State Park, VII-14-1998, J. B. Keiper, 1♂ (CMNH); **Lawrence**, Sharpes in Wayne National Forest, IX-10-1995, 1♂ (CMNH); **Lorain**, Amherst (Steyskal, 1959); **Muskingum**, Blue Rock State Forest, VII-14-1995, J. B. Keiper, 3♂ (CMNH); **Portage**, 4.5 miles E Kent, VI-25, VIII-15-1967, D. Trelka, 2♂ (CMNH); 7.0 miles E Kent, VI-24, VII-13, VIII-26-1964, E. J. Allen, 3♂ (CMNH); 7.0 miles N Kent, VII-10-1963, B. A. Foote, 2♀ (CMNH); **Ross**, no date/locality given, 1♂ (OSU); **Summit**, N. Cuyahoga Falls, VI-04-1967, G. Piper, 1♂ (CMNH); 1.0 mile N Peninsula, IX-03-1969, 1♀ (CMNH); **Tuscarawas**, 6.0 miles N Dover, VI-03-1968, W. B. Garnett, 1♂, 1♀ (CMNH).

Habitat: Floodplain forests, mesic forests.

Phenology: Multivoltine. Flight period in Ohio from occurs early June to early September. Overwinters as pupa in leaf litter.

Biology: Predator/parasitoid of the slug genera *Pallifera* and *Philomycus* (Trelka and Foote, 1970).

Immature Stages: E, P (Foote, 1961b).

60. *Tetanocera ferruginea* Fallén, 1820

General Distribution: Holarctic. NF to AK, south to NJ, OH, and CA.

Ohio Records (Figure 21L): **Champaign**, Cedar Swamp, IX-15-1964, J. L. Williams, 1♀ (OSU); **Lake**, Mentor Marsh, VIII-04-1981, no collector given, 1♀ (CMNH); **Portage**, Kent, VII-22-1965, W. H. Robinson, 5♂ (CMNH); 1.0 mile N Kent, III-26-1962, L. V. Knutson, 1♂ reared from floating puparium (CMNH); 1.0 mile N Kent, IX-07-1962, B. A. Foote, 1♂ (CMNH); 4.5 miles E Kent, V-12-1967, K. Valley, 1♂ (CMNH); 4.5 miles E Kent, VII-30-1967, B. A. Foote 1♂ (CMNH); 7.0 miles E Kent, V-15-1962, B. A. Foote, 2♂ (CMNH); 5.0 miles S Kent, V-25-1956, B. A. Foote, 2♂, 2♀ (CMNH); 6.0 miles SE Kent, IX-2, 6-1965, K. Valley, 3♂ (CMNH); 4.0 miles NW Kent, VI-15-1962, D. Miletich, 1♀ (CMNH); Mogadore Reservoir, IV-17-1962, B. A. Foote, 2♂ reared from floating puparia (CMNH); Streetsboro Bog, VIII-05-1964, R. C. McConnell, 1♂ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 4♂, 2♀ (CMNH); **Wayne**, 0.5 mile S Rittman, IX-09-1969, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, ponds, swamps.

Phenology: Multivoltine. Flight period in Ohio occurs from mid-April to late September. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate aquatic snails (Foote, 1999).

Immature Stages: E, L₁₋₃, P (Foote, 1961b); L₃, P (Rozkošný, 1965, 1967).

61. *Tetanocera fuscinervis* (Zetterstedt, 1838)

General Distribution: Holarctic. NF to AK, south to CT, OH, and AZ.

Ohio Records (Figure 22A): **Ashtabula**, near Ashtabula/Geauga border at Route 322, VI-07-2002, 1♂ (CMNH); **Portage**, Kent, VI-05-1967, D. Trelka, 1♂ (CMNH); 4.5 miles E Kent, III-16-1966, B. A. Foote, 7♂, 3♀ reared from floating puparia (CMNH); 4.5 miles E Kent, IV-22-1964, B. A. Foote, 1♀ reared from floating puparium (CMNH); 4.5 miles E Kent, V-30-1964, E. J. Allen, 2♂, 1♀ (CMNH); 4.5 miles E Kent, VI-5, VII-08, VIII-04, VIII-14-1967, D. Trelka, 3♂, 2♀ (CMNH); Herrick Fen, VI-16-1985, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, fens.

Phenology: Multivoltine. Flight period in Ohio occurs from late May to mid-August. Overwinters as pupa in floating puparium.

Biology: Larvae prey on pulmonate shoreline or stranded aquatic snails (Beaver, 1972; Foote, 1996a).

Immature Stages: E, L₁₋₃, P (Foote, 1961b, as *T. unicolor* Loew; Rozkošný, 1967).

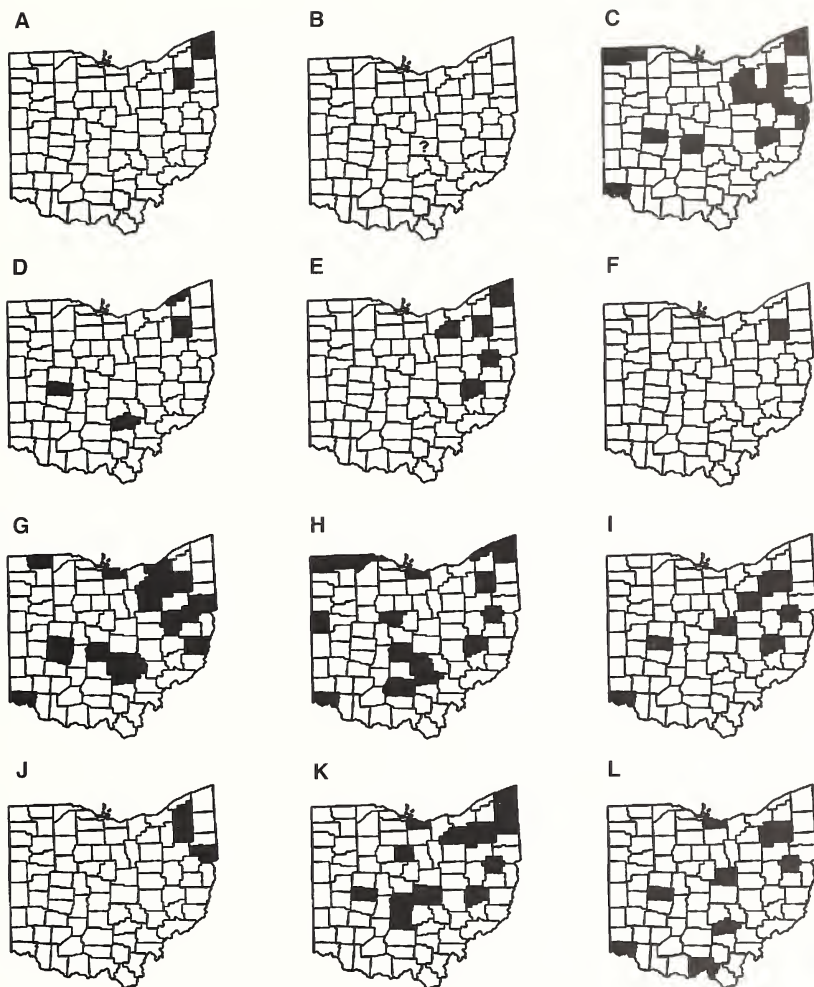


Figure 22. Distribution of Ohio Sciomyzidae. A, *Tetanocera fuscinervis*; B, *Tetanocera iowensis*; C, *Tetanocera loewi*; D, *Tetanocera melanostigma*; E, *Tetanocera montana*; F *Tetanocera oxia*; G, *Tetanocera plebeja*; H, *Tetanocera plumosa*; I, *Tetanocera rotundicornis*; J, *Tetanocera valida*; K, *Tetanocera vicina*; L, *Trypetoptera canadensis*.

62. *Tetanocera iowensis* Steyskal, 1938

General Distribution: Nearctic. IA, MO, OH.

Ohio Records (Figure 22B): (Steyskal, 1959; no specific locality given).

Habitat: Unknown.

Phenology: Unknown.

Biology: Unknown.

Immature Stages: None described.

63. *Tetanocera loewi* Steyskal, 1959

General Distribution: Nearctic: ON to BC, south to KY, CO, and CA.

Ohio Records (Figure 22C): **Ashtabula**, Ashtabula, no date/locality data given, 1♂ (OSU); Pymatuning Creek Fen, VI-21-2001, J. B. Keiper, 1♂ (CMNH); **Carroll**, Specht Marsh, VII-19-1964, R. E. McConnell, 5 (CMNH), Specht Marsh, VII-27-1964, E. J. Allen, 13 (CMNH); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 1♂ (CMNH); Cedar Swamp, VII-11, VIII-4-1964, J. L. Williams, 3♂ (OSU); **Crawford**, Galion, VI, no collector recorded, 1♂ (OSU) **Franklin**, Columbus, J. S. Hine, 1♂, 3♀ (OSU); **Guernsey**, 11.0 miles S. Cambridge, IV-04-1965, E. J. Allen, 5 (CMNH); **Hamilton**, Cincinnati, VI-21-1974, W. Downing, 1♂ (CMNH); **Jefferson**, VIII-1908, R. Sim, 1♂ (OSU); **Medina**, 3.0 miles W. Wadsworth, VIII-06-1964, E. J. Allen, 3 (CMNH); **Portage**, Kent, VII-13-1965, W. H. Robinson, 1♂ (CMNH); 1.0 mile N Kent, VII-02-1964, E. J. Allen, 1♂ (CMNH); 2.0 miles N Kent, IX-07-1962, B. A. Foote, 2♂ (CMNH); 4.0 miles N Kent, VI-15-1963, B. A. Foote, 8 (CMNH); 4.5 miles E Kent, VI-29, VIII-27-1964, E. J. Allen, 1♂, 1♀ (CMNH); 6.0 miles E Kent, VII-09-1967, J. Novak, 1♂ (CMNH); Lake Hodgson, VI-20-1996, J. B. Keiper, 1♂, 1♀ (CMNH); Streetsboro Bog, IX-26-1962, B. A. Foote, 2♂, 1♀ (CMNH); Dollar Lake near Twin Lakes, VI-20-1962, D. Miletich, 1♂ (CMNH); **Stark**, VIII-16-1964, B. A. Foote, 2♂ (CMNH); **Wayne**, Wooster, VIII-19-1907, 1♂ (OSU); **Williams**, Dehnis Swamp in Florence Township, VI-11, IX-09-1950, H. E. Price, 3♀ (OSU).

Habitat: Marshes, fens, ponds, swamps.

Phenology: Univoltine. Flight period in Ohio occurs from early April to late September. Overwinters as unhatched first instar within egg.

Biology: Larvae prey on pulmonate aquatic snails (Foote, 1999).

Immature Stages: E, L₁₋₃, P (Foote, 1961b).

64. *Tetanocera melanostigma* Steyskal, 1959

General Distribution: Nearctic. NF to SK, south to CT, IL, and CO.

Ohio Records (Figure 22D): **Champaign**, Cedar Swamp, V-31-1961, R. E. Woodruff, (FSCA); **Hocking**, "Neotoma," VI-10-1958, C. A. Triplehorn, 1♀ (OSU); no locality given, VI-08-1956, F. W. Mead, 2♂, 2♀ (FSCA); **Lake**, Mentor Marsh, A. D. Hury, 3♂ (CMNH); **Portage**, 1.0 mile E Kent, VI-25-1998, B. A. Foote, 1♂ (CMNH), Towners Woods, VI-01-1996, B. A. Foote, 1♂ (CMNH).

Habitat: Marshes, moist forests.

Phenology: Multivoltine. Flight period in Ohio occurs from late May to late June. Overwinters as pupa in puparium in leaf litter.

Biology: Larvae are predators/parasitoids of land snails belonging to the genus *Succinea* (Foote, 1996b).

Immature Stages: E, L₁₋₃, P (Foote, 1961b).

65. *Tetanocera montana* Day, 1881

General Distribution: Holarctic; ON to AK, south to NY, OH, and WY.

Ohio Records (Figure 22E): **Ashtabula**, Pymatuning Creek Wetland, V-27-1997, B. A. Foote, 1♂ (CMNH); **Carroll**, Specht Marsh, VI-28-1964, E. J. Allen, 1♂ (CMNH); **Guernsey**, 11.0 miles S Cambridge, VII-31-1964, R. C. McConnell, 1♂ (CMNH); **Medina**, 3.0 miles W Wadsworth, VIII-06-1964, E. J. Allen, 1♂ (CMNH); **Portage**, 3.0 miles W Kent, VII-21-1965, B. A. Foote, 1♂ (CMNH).

Habitat: Woodland ponds, swamps, marshes.

Phenology: Univoltine. Flight period in Ohio occurs from late May to early August. Overwinters as first instar within egg membranes or as young larvae.

Biology: Larvae prey on pulmonate aquatic snails (Foote, 1999).

Immature Stages: E, L₁₋₃, P (Foote, 1961b).

66. *Tetanocera oxia* Steyskal, 1959

General Distribution: Nearctic. AB, BC, MB, NF, SK; CO, CT, MI, MN, MT, NY, OH, WY.

Ohio Records (Figure 22F): **Portage**, Kent, VIII-02-1967, D. Trelka, 1♂ (CMNH); 4.5 miles E Kent, VI-01-1968, B. A. Foote, 1♂ (CMNH); 7.0 miles E Kent, IV-20-1964, E. J. Allen, 1♂ reared from puparium (CMNH).

Habitat: Marshes.

Phenology: Multivoltine. Flight period in Ohio occurs from late April to early August. Overwinters as pupa.

Biology: Larvae are parasitoids or predators of land snails belonging to the genus *Catinella* (Foote, 1996b).

Immature Stages: P (Foote, 1961b).

67. *Tetanocera plebeja* Loew, 1862

General Distribution: Nearctic. Transcontinental to AK, south to CT, AZ, and CA.

Ohio Records (Figure 22G): **Belmont**, Bethesda, V-25-1974,

B. A. Foote, 1♂ (CMNH); VI-25-1975, B. A. Foote, 1♂ (CMNH); **Carroll**, Specht Marsh, VII-19-1964, R. E. McConnell, 1♂ (CMNH); **Champaign**, Cedar Swamp, V-31-1961, R. E. Woodruff, 1♂ (FSCA); VII-07-1962, R. E. Woodruff, 1♂ (FSCA); **Columbiana**, Beaver Creek State Park, VII-08-1996, J. B. Keiper, 1♂ (CMNH); **Cuyahoga**, Bedford, VII-02-1923, J. C. Pallister, 1♀ (CMNH); **Erie**, Sandusky, no date given, 1♂ (OSU); **Fairfield**, no further data given, 1♂ (Steyskal, 1959); **Franklin**, Columbus, no date given, 1♂ (OSU); **Fulton**, Wauseon, IX-05-1930, J. S. Hine, 1♀ (OSU); **Hamilton**, Cincinnati, VIII-10, IX-04-1974, W. Downing, 1♂, 1♀ (CMNH); **Hocking**, "Neotoma," VI-10-1958, C. A. Triplehorn, 1♀ (OSU); no date, locality, or collector given, 1♂ (OSU); **Logan**, no locality given, VII-14-1930, J. Patton, 1♂ (UMN); **Medina**, 2.0 miles W Wadsworth, VIII-01-1964, W. B. Stoltzfus, 1♂ (CMNH); 3.0 miles W Wadsworth, VIII-06-1964, W. B. Stoltzfus, 2♂ (CMNH); 6.0 miles S Wadsworth, VI-27, 1964, W. B. Stoltzfus, 1♂ (CMNH); **Perry**, no further data given (Steyskal, 1959); **Portage**, 1.0 mile N Kent, VII-08-1964, W. B. Stoltzfus, 1♂ (CMNH); 3.0 miles N Kent, VIII-05-1964, E. J. Allen, 1♂ (CMNH); 5.0 miles S Kent, VI-22-1964, E. J. Allen, 1♂ (CMNH); 5.0 miles SE Kent, VIII-31-1964, E. J. Allen, 1♂ (CMNH); 15 miles N Kent, VI-15-1964, E. J. Allen, 1♂ (CMNH); 16 miles NE Kent, VI-25-1964, E. J. Allen, 1♂ (CMNH); 4.5 miles E Kent, III-16-1966, B. A. Foote, 5 adults reared from floating puparia (CMNH); Streetsboro Bog, VII-10-1964, B. A. Foote, 1♂ (CMNH); **Summit**, Ira, no further data given, J. S. Hine, 1♂ (OSU); Twinsburg, VI-10-1931, no collector given, 2♂ (CMNH); **Tuscarawas**, 6.0 miles N Dover, VI-03-1968, W. B. Garnett, 3♂ (CMNH); **Wayne**, Wooster, VI-02-1951, no collector given, 1♂ taken at light (OSU); Browns Lake Bog near Shreve, VI-21-1959, C. A. Triplehorn, 1♀ (OSU).

Habitat: Marshes, fens, swamps, floodplain forests, mesic forests, old fields.

Phenology: Multivoltine. Flight period in Ohio occurs from late May to mid-September. Overwinters as pupa in leaf litter.

Biology: Larvae are parasitoids or predators of the slug *Deroceras laeve* (Müller) (Trelka and Foote, 1970; Trelka and Berg, 1977).

Immature Stages: E, L₁, P (Foote, 1961b), E, L₁₋₃, P (Trelka and Foote, 1977).

68. *Tetanocera plumosa* Loew, 1847

General Distribution: Nearctic; transcontineantal, south to

NC, TX and northern MEX.

Ohio Records (Figure 22H): **Ashtabula**, near Ashtabula/Gauga border at Route 322, VI-07-2002, J. B. Keiper, 1♂ (CMNH); Ashtabula, no date or collector given, 1♀ (OSU); **Carroll**, 3.0 miles E Carrollton, VII-17-1964, R. E. McConnell, 2♂ (CMNH); Specht Marsh, VII-19-1964, R. E. McConnell, 5 (CMNH); **Erie**, Sandusky, VII-1914, J. S. Hine, 1♀ (OSU); **Franklin**, Blendon Woods Metro Park, VI-07-1961, F. W. Mead, 1♂ (FSCA); **Fulton**, Wauseon, J. S. Hine, VIII-25-1902, IX-05-1903, 1♂, 1♀ (OSU); **Guernsey**, 11.0 miles S Cambridge, IV-04-1965, E. J. Allen, 7 (CMNH); **Hamilton**, Cincinnati, IX-04-1974, W. Downing, 1♂ (CMNH); **Hocking**, no locality given, V-25-1930, 3♂ (OSU); **Lake**, Holden Arboretum, VII-10-1996, B. A. Foote, 1♂ (CMNH); **Lucas**, 6.0 miles W Toledo, VIII-20-1938, I. J. Cantrall 1♂ (FSCA); **Marion**, Marion, VI-13-1941, R. C. Osburn, 1♂ (OSU); **Portage**, Kent, VII-13-1965, W. H. Robinson, 1♂ (CMNH); Dollar Lake near Twin Lakes, VI-20-1962, D. Miletich, 1♀ (CMNH); 1.0 mile N Kent, IX-07-1962, B. A. Foote, 1♂ (CMNH); 3.0 miles N Kent, VIII-05-1965, B. A. Foote, 1♂ (CMNH); 4.0 miles N Kent, VI-15-1962, D. Miletich, 1♂ (CMNH); Ravenna, VI-22-1964, E. J. Allen 1 third-instar larva (CMNH); West Branch State Park, VII-03-1993, B. A. Foote, 1♂ (CMNH); **Ross**, no further data (Steyskal, 1959); **Washington**, Marietta, no further data given (Steyskal, 1959); **Williams**, no further data (Steyskal, 1959).

Habitat: Marshes, fens, swamps, roadside ditches.

Phenology: Univoltine. Flight period in Ohio occurs from early April to early September. Overwinters as third instar.

Biology: Larvae prey on shoreline and aquatic pulmonate snails (Foote, 1961, as *T. nanciae* Steyskal).

Immature Stages: E, L₁₋₃, P (Foote, 1961b, as *T. nanciae*).

69. *Tetanocera rotundicornis* Loew, 1861

General Distribution: Nearctic. Transcontinental, south to NC, TN, and UT.

Ohio Records (Figure 22I): **Carroll**, Specht Marsh, VII-19-1964, R. E. McConnell, 1♂ (CMNH); Specht Marsh, VII-27-1964, E. J. Allen, 2♀ (CMNH); **Champaign**, Cedar Swamp, V-31-1954, R. E. Woodruff, 1♂ (FSCA); **Guernsey**, 11.0 miles S Cambridge, IV-04-1965, E. J. Allen, 7 (CMNH); **Hamilton**, Cincinnati, IX-04-1974, W. Downing, 1♂ (CMNH); **Knox**, Danville, VI-09-1899, 1♂, 1♀ (OSU); **Portage**, 1.0 mile N Kent, VI-01-1963, B. A. Foote, 1♀ (CMNH); 4.0 miles NW Kent, VI-15-1962, D. Miletich, 1♀ (CMNH); 4.5 miles E Kent,

VII-02-1963, VII-21-1965, B. A. Foote, 3 (CMNH); Dollar Lake near Twin Lakes, IV-30-1963, B. A. Foote, 1♂ (CMNH); **Summit**, Akron, VI-1916, J. S. Hine, 1♀ (OSU); **Wayne**, Wooster, VI-12-1959, C. A. Triplehorn, 1♂, 1♀ (OSU).

Habitat: Marshes, fens, moist fields, drainage ditches.

Phenology: Multivoltine. Flight period in Ohio occurs from late April to mid-July. Overwinters as pupa.

Biology: Larvae are parasitoids or predators of land snails of the genus *Oxyloma* (Berg, 1953; Foote, 1996b).

Immature Stages: E, L₁₋₂, P (Foote, 1961b).

70. *Tetanocera valida* Loew, 1862

General Distribution: Nearctic. NF to BC, south to CT, IL, and CO.

Ohio Records (Figure 22J): **Columbiana**, Beaver Creek State Park, VII-10-1996, J. B. Keiper, 1♂ (CMNH); **Portage**, Kent, V-28-1967, D. Trelka, 1♂ (CMNH); 4.5 miles E Kent, VI-17-1965, B. A. Foote, 1♂ (CMNH); 4.5 miles E Kent, VIII-10, 29-1967, D. Trelka, 2♂ (CMNH); 4.5 miles E Kent, IX-15-1966, R. Miller, 1♂ (CMNH); 6.0 miles E Kent, VII-10-1963, B. A. Foote, 1♀ (CMNH); 7.0 miles E Kent, VII-02-1962, B. A. Foote, 6♂, 9♀ (CMNH); Streetsboro Bog, VII-08-1964, R. V. McConnell, 1♂ (CMNH); **Geauga**, Fern Lake Bog, VII-07-2002, E. Chapman, 1♂ (BAF).

Habitat: Swamps, floodplain forests, mesic forests, shrubby marshes.

Phenology: Multivoltine. Flight period in Ohio occurs from late May to mid-September. Overwinters as pupa in litter.

Biology: Larvae are parasitoids or predators of the slug *D. laevis* (Trelka and Foote, 1970).

Immature Stages: E, L₁ (Foote, 1961b).

71. *Tetanocera vicina* Macquart, 1843

General Distribution: Nearctic. NF to BC, south to NC, NM, and CA.

Ohio Records (Figure 22K): **Ashtabula**, Fall, 1921, J. S. Hine, 1♀ (OSU); **Champaign**, Cedar Swamp, VI-17-1961, B. A. Foote, 2♂, 1♀ (CMNH); Cedar Swamp, VII-11, VIII-04, X-08-1963, J. L. Williams, 3♂ (OSU); **Carroll**, Specht Marsh, VII-19-64, R. C. McConnell, 1♂ (CMNH); **Crawford**, Galion, VI, no collector given, 1♂ (OSU); **Erie**, Sandusky, VI-15-1924, no collector given, 1♂ (OSU); **Franklin**, Columbus, no date/locality data given, 1♂ (OSU); **Guernsey**, 11.0 miles S Cambridge, IV-04-1965, E. J. Allen, 1♂ (CMNH); **Licking**, Newark, no collector given, 2♂ (OSU); **Medina**, no date/locality data given, 1♀ (OSU); **Pickaway**, no further data given (Steyskal, 1959); **Portage**, Aurora, VIII-24-1923, J. C. Pallister, 1♀ (CMNH); Kent, VIII-30-1967, D.

Trelka, 1♂ (CMNH); 4.5 miles E Kent, III-16-1966, B. A. Foote, 1 third instar (CMNH); 8.0 miles SE Kent, VI-11-1964, E. J. Allen, 1♂ (CMNH); 4.5 miles E Kent, VIII-29-1967, D. Trelka, 1♀ (CMNH); 4.0 miles NW Kent, VI-15-1962, D. Miletich, 2♂, 1♀ (CMNH); 7.0 miles N Kent, VII-09-1963, B. A. Foote, 1♂ (CMNH); 16.0 miles NE Kent, VI-25-1964, E. J. Allen, 1♂ (CMNH); **Summit**, Cuyahoga Falls, no further data given (Steyskal, 1959); Cuyahoga Valley National Park (then Cuyahoga Valley National Recreation Area), VII-02-1998, B. A. Foote, 1♂ (CMNH); **Wayne**, 2.0 miles NE Wadsworth, VI-30-1964, W. B. Stoltzfus, 1♂ (CMNH).

Habitat: Marshes, fens, roadside ditches, swamps.

Phenology: Univoltine. Flight period in Ohio from early April to late September. Overwinters as larva.

Biology: Larvae prey on pulmonate aquatic snails (Foote, 1999).

Immature Stages: E, L₁₋₃, P (Foote, 1961b).

72. *Trypetoptera canadensis* (Macquart, 1843)

General Distribution: Nearctic. ON to BC, south to NC, CO, and NM.

Ohio Records (Figure 22L): **Carroll**, 3.0 miles E Carrollton, VII-17-1964, R. E. McConnell, 1♀ (CMNH); Specht Marsh, VII-17-1964, E. J. Allen, 1♀ (CMNH); **Champaign**, VI-17-1961, B. A. Foote, 2♀ (CMNH); **Erie**, Cedar Point near Sandusky, V-30-1903, J. S. Hine, 2♀ (OSU); **Hamilton**, Cincinnati, VI-13-1902, J. S. Hine, 4♀ (OSU); **Hocking**, "Neotoma," VI-10-1958, C. A. Triplehorn, 2♀ (OSU); 7.0 miles S Lancaster, VI-04-1977, L. E. Watrous, 2♂, 1♀ (OSU); no locality given, VI-02-1957, F. W. Mead, 2♂ (FSCA); **Knox**, Danville, V-19-1899, J. S. Hine, 1♀ (OSU); **Scioto**, no locality given, VI-09-1945, D. J. and J. N. Knull, 1♂ (OSU); **Summit**, Ira, no date given, J. S. Hine, 1♀ (OSU).

Habitat: Floodplain forests, mesic forests, marshes, fens.

Phenology: Voltinism unknown. Flight period in Ohio occurs from late May to late July. Overwintering habits unknown.

Biology: Largely unknown. Preliminary data show that larvae prey on small pulmonate land snails (B. A. Foote, unpublished data).

Immature Stages: None described.

Discussion

Of the 21 genera of snail-killing flies found in the Nearctic region (Knutson, 1987), only *Sepedomerus* (Steyskal, 1973) (one species, *S. macropus* (Walker, 1849)) is not found in the Ohio region. This species has a southerly distribution and is more prominent in areas south of North America (Knutson et al., 1986, p. 28).

Over 200 species of Sciomyzidae from nearly all of the major biogeographic realms of the world have now been reared (Berg and Knutson, 1978; Knutson, 1987; B. A. Foote, unpublished data). Nearly all have larvae that prey exclusively on members of the molluscan classes Gastropoda and Pelecypoda, and a considerable amount of adaptive radiation with respect to larval food preference has occurred. Fifteen feeding guilds (behavioral groups) have been recognized recently in the world fauna (Knutson and Vala, 2002), and nine of these feeding guilds can be recognized in the 72 species occurring in Ohio. These guilds are briefly described below:

Predators/parasitoids or saprophages of dead, moribund, or living snails on damp surfaces

A single Ohio species (1.4 percent of Ohio species), *Atrichomelina pubera*, belongs to this feeding guild. Feeding habits within this guild vary from being truly saprophagous on dead and decaying snails to active predation on actively moving snails occurring on moist surfaces. The feeding habits of *A. pubera* appear to be exclusively scavenging.

Parasitoids of aestivating aquatic snails on exposed surfaces

This is a very small guild of highly specialized sciomyzids that are intimately associated with aestivating pulmonate aquatic snails in wetland habitats. Eggs are placed directly on the shell of the host snail, and the entire larval life is usually spent within one host. Only *Sciomyza varia* (1.4 percent of Ohio species), a parasitoid of lymnaeid snails, belongs to this guild in Ohio.

Parasitoids of amber snails of the family Succineidae

The habit of utilizing wetland and terrestrial snails of the family Succineidae in a more parasitoid manner is not well developed in the Sciomyzidae, and only a few North American species fall into this category. The relationship with the food snail is much more intimate than it is with the terrestrial predators. Adult females usually deposit eggs only on or very close to the larval host, and each larva commonly completes its entire life within one snail. In Ohio, this guild is composed of *Pherbellia schoenherri maculata*, *Sciomyza aristalis*, *Tetanocera melanostigma*, *T. oxia*, and *T. rotundicornis* (6.9 percent of Ohio species).

Predators of snail eggs

Only three Ohio species of *Antichaeta* are known to have larvae that prey on snail eggs. Female flies lay their eggs directly on gelatinous egg masses, and the newly hatched larvae begin attacking the enclosed eggs. Older larvae frequently move from one egg mass to another. Puparia are formed on soil away from the egg masses. In Ohio, *Antichaeta borealis*, *A. fulva*, and *A. melanosoma* belong to this guild (4.2 percent of Ohio species).

Parasitoids of pulmonate terrestrial snails

A small group of the North American sciomyzid species occurs in terrestrial habitats where their larvae attack land snails. Females of species belonging to this guild lay eggs on low vegetation or surface litter in habitats harboring food snails. Younger larvae typically feed singly within one host for several days to a week or more, but then abandon the snail after killing it and seek out additional prey. Usually two to five gastropods satisfy the nutritional needs of each larva. Pupation usually occurs in surface litter. Only three Ohio species are known to compose this guild: *Oidemantops ferrugineus*, *Pherbellia albovaria*, and *Pteromicra steyskali* (4.2 percent of Ohio species).

Predators of pulmonate terrestrial snails

Larvae of the single Ohio species (1.4 percent) having this feeding habit, *Trypetoptera canadensis*, appear to feed in a more predacious manner on small land snails. Preliminary observations show that newly hatched larvae remain with their prey for extended periods of time, but older larvae become more predacious and attack a number of snails before completing larval life (B. A. Foote, unpublished data).

Parasitoids/predators of slugs

Three (4.2 percent) Ohio species feed on slugs. Larvae of *T. plebeja* and *T. valida* prey on slugs belonging to the genus *Deroceras*, whereas those of *T. clara* attack slugs of the genera *Pullifera* and *Philomycus*.

Predators of aquatic snails

The aquatic predators form a distinctive group of species having larvae that attack pulmonate snails of the families Lymnaeidae, Physidae, and Planorbidae. Larvae of the Ohio species in this guild are not fully aquatic, because they usually remain in contact with the water surface and breathe atmospheric air. In general, they prey on aquatic snails that glide along the under side of the surface film. The larvae seemingly are nonselective in their choice of prey species except that they seem unable to attack operculate snails. Each larva can kill between 10 and 35 snails depending on the size of prey available. Younger larvae are restricted to prey measuring only a few mm in size, but older larvae can overcome snails measuring 10–20 mm in greatest diameter. The following 25 species (34.7 percent) of Ohio Sciomyzidae are known to be predators of aquatic snails: *Dicrya atlantica*, *D. borealis*, *D. expansa*, *D. ludsonica*, *D. pictipes*, *D. sabroskyi*, *D. steyskali*, *D. stricta*, *D. texensis*, *Elgiva sollicita*, *Sepedon arripes*, *S. borealis*, *S. fuscipennis*, *S. gracilicornis*, *S. lignator*, *S. neili*, *S. pusilla*, *S. spinipes americana*, *S. tenuicornis*, *Tetanocera amae*, *T. ferruginea*, *T. loewi*, *T. montana*, *T. plumosa*, and *T. vicina*.

Predators of fingernail clams

Among the North American Sciomyzidae, only larvae of species of *Renocera* are known to prey on fingernail clams of the family Sphaeriidae. Eggs are laid on shoreline vegetation and litter. In contrast to nearly all other aquatic Sciomyzidae, newly hatched larvae of *Renocera* leave the surface film and seek out completely submerged prey. The first instar usually remains within the mantle cavity of a clam for 4–6 days before killing it. Older larvae are more predacious and can kill up to 25 prey before pupating. In Ohio, *Renocera ananda*, *R. brevis*, and *R. longipes* belong to this trophic guild (4.2 percent of Ohio species).

Little to nothing is known of the life histories, larval feeding habits, and immature stages of 13 species of Ohio Sciomyzidae: *Pherbellia luctifera*, all 11 species of *Limnia*, *Tetanocera iowensis*, and *Poecilographa decora*. This list represents 22.2 percent of the known sciomyzid fauna of the state.

Many of the records we report are more than 30 years old, and some species have not been collected in Ohio since the 1960s. Ohio has undergone rapid changes since the early collecting by scientists such as J. Hine of Ohio State University during the early 1900s, and even during the time of later entomologists such as BAF and JBK, E. J. Allen, E. G. Chapman, A. D. Huryn, C. A. Triplehorn, and K. R. Valley. The lack of recent records of certain species (e.g., *Antichaeta borealis*, *Dictya borealis*, *D. hudsonica*, and *Tetanocera oxia*) may be due to rarity, natural population fluctuations, habitat loss, persistent drought conditions, loss of natural prey, or other factors. All species are reliant upon aquatic habitats or moist woodlands and these areas have undergone significant alteration and destruction due to extensive residential, commercial, and industrial development. Further collecting of Sciomyzidae and their deposition into established collections will be necessary for the continued documentation of species occurrence in Ohio and other areas of the midwest. Loss of sciomyzid species that were once collected with some frequency in Ohio should be viewed as a possible indicator of loss or degradation of natural habitat.

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This paper is dedicated to the fond memory of the late C. O. Berg of Cornell University, who stimulated many students throughout the world to initiate biological studies of the family Sciomyzidae.

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PALEOCLIMATIC INFERENCE FROM MORPHOLOGICAL STRUCTURE IN THE SNAIL *GASTROCOPTA PROCERA* (GASTROPODA: PUPILLIDAE)

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ABSTRACT

This study describes relationships between morphometric parameters of Cenozoic populations of *Gastrocopta procera* (Gould, 1840) and climatic variables for the north central United States over which the snail is currently distributed. We use the multivariate techniques of principal components analysis and multiple linear regression to illustrate how the response of snail structure to climatic variation in extant populations can be used to predict climatic conditions for fossil populations. Five Pliocene populations of *G. franzenae* Taylor, 1960, two Holocene populations of *G. riograndensis* (Pilsbry and Vanatta, 1900) and one of *G. cristata* (Pilsbry and Vanatta, 1900) also were studied. Four climatic variables (latitude, longitude, total annual precipitation, and number of frost-free days) have a highly significant predictive value for the major axis of morphological variation in extant populations of *G. procera*. This axis accounts for more than half of the structural variation among 339 specimens sampled from 31 extant populations across the biogeographic range of the species. Extrapolation of relationships between morphological structure and modern climatic conditions to fossil populations strongly suggests that the populations represented by fossils lived in conditions similar to those now present in the southern parts of the range of *G. procera*. These analyses imply that populations of the putative ancestral species, *G. franzenae*, may have lived under conditions warmer and wetter than those of present-day populations of the descendant species.

Introduction

The primary purpose of this paper is to demonstrate relationships between morphometric parameters of populations of a snail and climatic variables for the continental region over which the snail is distributed. We illustrate how the response of snail structure to climate in extant populations can be used to predict climatic conditions for fossil populations of this snail.

Paleoclimatic reconstructions using nonmarine molluscs typically assume that climate is a major factor controlling their distributions (Hibbard and Taylor, 1960, p. 16–19; Taylor, 1960, p. 4–9; Sparks, 1961; Lozek, 1964, p. 49–53; Harris and Pip, 1973; Baerreis, 1980; Miller and Kay, 1981; Keen, 1990). Only rarely have these assumptions been subjected to quantitative analysis. We are aware of only one such study in North America, involving the terrestrial pulmonate gastropod, *Gastrocopta procera* (Gould, 1840), a statistical analysis which suggested that some of the variation in shell morphology appeared to be related to climatic variables (Couri, 1976).

Gastrocopta procera and the closely related species *G. cristata* (Pilsbry and Vanatta, 1900) are extant species with relatively broad distributions in the eastern United States (Pilsbry, 1948, p. 907, p. 913; Hubricht, 1985, p. 72). They are also common as fossils in many of the Pleistocene molluscan faunas reported from the southern Great Plains (Hibbard and Taylor, 1960, p. 10; Taylor, 1965, p. 607; Miller, 1976). Another common Holocene species, *G. riograndensis* (Pilsbry and Vanatta, 1900, p. 595), is also morphologically similar to *G. procera*.

Some of the morphological shell characters that distinguish *G. procera* and *G. cristata* from each other have been found occurring together in many individuals from several different Pliocene fossil localities. Taylor (1960, p. 67–69) considered the morphological overlap in these Pliocene shells to justify a new species, *G. franzenae*, and suggested that *G. franzenae* was the probable ancestral species that evolved into *G. procera* and *G. cristata* during the Pleistocene. If true, this would be one of the few known examples documenting the evolution of a new terrestrial pulmonate snail species during the Pleistocene.

Our investigation started as a study of the nature and magnitude of the evolutionary changes in shell morphology that could be measured in the fossil shells of *G. procera* from the Pleistocene faunas of the southern Great Plains (Couri, 1976). *Gastrocopta procera* was chosen for study because its shell characteristics permitted unequivocal identification to species (Figure 1) and the availability of both modern and fossil materials for study in museum collections.

The range of shell variation was evaluated in recent populations of *G. procera* from 14 localities over much of its modern range in the continental United States. Measurements were made of the several aspects of shell

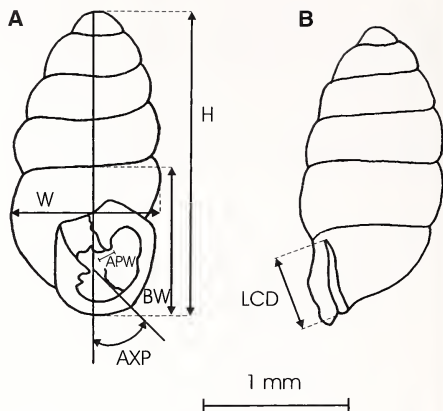


Figure 1. Diagram of a *Gastrocopta procera* specimen showing the primary morphometric landmarks and variables. A, ventral view; B, lateral view. Abbreviations and definitions of parameters are given in Table 2.

morphology that have been used to distinguish various members of this cluster of species. Preliminary results from this phase of the study yielded statistically significant correlations between particular morphological measurements with certain climatic parameters, such as temperature and precipitation, for the collection sites (Couri, 1976). The potential usefulness of these shell-climate interrelationships for paleoenvironmental reconstructions led to an expansion of this study into the current report.

Materials and Methods

Samples from Holocene populations of the snail *Gastrocopta procera* were obtained from 31 localities across the current geographic range of the species (Table 1); a total of 614 specimens were used in various analyses. Museum lots were selected for which there was reasonable certainty that the specimens were collected alive and at their living site. Thus, stream drift material, although abundant in museum collections, was excluded. In addition to these representatives of *Gastrocopta procera*, samples were obtained of five Pliocene populations of *G. franzenae* (a total of 141 specimens), two Holocene populations of *G. riograndensis* (37 specimens), and one Holocene population of *G. cristata* (29 specimens).

All specimens were cleaned and body remnants removed by soaking in 50 percent household bleach solution, using ultrasonic agitation as necessary. Only mature specimens, as judged by the presence of lamellae within

Table 1. Sampling localities, codes, and sample sizes. Samples A through AE represent populations of *Gastrocopta procera*; samples 1–5 are of *G. franzenae*; samples r and g belong to *G. riograndensis*; and sample c belongs to *G. cristata*. Museum abbreviations are as follows: KSU, Kent State University, Department of Geology; MCZ, Museum of Comparative Zoology, Harvard University; UMMZ, University of Michigan Museum of Zoology.

Code	Sample size	Museum lot no.	Geographic location	Lat. (N)	Long. (W)
A	22	UMMZ 106898	Orange Co. VA	38° 15.6'	77° 59.8'
B	30	MCZ 54573	Dallsville MD	38° 34.2'	76° 04.7'
C	13	MCZ 95876 & MCZ 46852	Knoxville TN	35° 58.1'	83° 55.1'
D	30	MCZ 3851 & UMMZ 106894	Cincinnati OH	39° 06.0'	84° 30.8'
E	21	MCZ 9659	Albion IL	38° 22.6'	88° 03.5'
F	24	MCZ 94679	St. Louis Co. MO	38° 37.0'	90° 11.6'
G	12	UMMZ 106905	Calceira AL	33° 16.4'	86° 42.5'
H	7	UMMZ 106955	Trego Co. KS	38° 54.6'	99° 52.8'
I	18	KSU 1970	Ellis Co. KS	38° 54.6'	99° 19.5'
J	26	KSU 7460	Beaver Co. OK	36° 43.7'	100° 31.3'
K	12	UMMZ 106928	Beaver Co. OK	36° 43.7'	100° 31.3'
L	30	UMMZ 106932	Wichita Mtns OK	34° 51.0'	98° 27.8'
M	30	UMMZ 106926	Dundee TX	33° 35.7'	98° 41.5'
N	30	UMMZ 165464	Comfort TX	29° 57.0'	98° 39.8'
O	11	MCZ 98221	Bear Creek AL	32° 20.3'	87° 12.1'
P	30	MCZ 3849	Washington DC	38° 53.5'	77° 02.0'
Q	24	USNM 474086	Yorktown VA	37° 14.1'	76° 30.4'
R	24	USNM 448536	Wilmington NC	34° 14.2'	77° 55.4'
S	16	USNM 68744	Nashville TN	36° 09.8'	86° 46.7'
T	13	USNM 231926	Kansas City MO	39° 06.0'	94° 34.7'
U	24	USNM 416301	Lincoln NB	40° 49.4'	96° 41.1'
V	15	USNM 424002	Topeka KS	39° 03.1'	95° 40.2'
W	24	USNM 520233	Sayre OK	35° 17.7'	99° 38.4'
X	8	USNM 536571	Colman TX	31° 44.5'	99° 29.1'
Y	24	USNM 448585	Amarillo TX	35° 12.5'	101° 50.0'
Z	11	USNM 102555	Lee TX	30° 17.1'	96° 57.7'
AA	12	USNM 511718	Lee TX	30° 17.1'	96° 57.7'
AB	24	USNM 106948	Grant LA	31° 34.7'	92° 31.1'
AC	13	USNM 473858	Colbert AL	34° 43.9'	87° 49.0'
AD	12	USNM 448594	Mobile AL	30° 41.3'	88° 02.6'
AE	24	USNM 511230	Indianapolis IN	39° 46.2'	86° 09.3'
1	30	UMMZ 183033	Meade Co. KS	37° 00.7'	100° 32.0'
2	30	KSU 0046	Meade Co. KS	37° 00.7'	100° 32.0'
3	21	UMMZ 183001	Oldham Co. TX	35° 34.8'	102° 29.3'
4	30	UMMZ 184153	Seward Co. KS	37° 03.0'	100° 55.8'
5	30	UMMZ 183068	Meade Co. KS	37° 14.4'	100° 21.6'
r	14	UMMZ 106957	Valles MX	21° 15.0'	99° 26.0'
g	23	UMMZ 34269	Brownsville TX	25° 54.0'	97° 30.0'
c	29	KSU 7461	Sayre OK	35° 17.6'	99° 39.1'

Table 2. Morphometric parameters, climatic variables, and their abbreviations.

Variable	Unit	Description
H	mm	height of shell, from apex to reflected peristome, along columellar axis
W	mm	width of shell, measured perpendicular to the body axis
WL	count	number of whorls, to nearest quarter-revolution
APW	mm	maximum angulo-parietal lamellar width
AXP	°	angle between columellar axis and axis of lower palatal lamella
LCD	mm	lip-crest distance, from aperture lip edge to crest axis
BW	mm	height of body whorl, from outer edge of reflected peristome to suture between body whorl and second whorl
LAT	°N	latitude
LONG	°W	longitude
FROST	inches	average depth of frost penetration
TEMPAVE	°F	average annual temperature
TEMPJL	°F	average July temperature
PRECSUM	inches	average summer precipitation
PRECAVE	inches	average annual precipitation
FFREE	days	average number of frost-free days
LASTKILL	date	average day of last killing frost in Spring
FIRSTKILL	date	average day of first killing frost in Fall
CLOUDY	days	average number of cloudy days per year

the aperture and the crest on the external labium, were used. Cleaned, mature specimens were mounted in 60-division faunal slides with gum-tragacanth solution. Using a Gaertner coordinate microscope (with “flat” optics), specimens were mounted with the aperture up and the rim of the peristome as horizontal as possible.

Morphometric data for all specimens were collected by a single observer using a Gaertner coordinate micrometer. Figure 1 illustrates key structural features of this snail used to define the corresponding morphometric variables. Table 2 gives the list of measurements and their abbreviations; however, three parameters (APW, LCD, and BW) were not measured for all of the populations, as noted in subsequent tables. In order to measure LCD, specimens were rotated 90° clockwise and remounted with the aperture to the left and the aperture rim vertical (as shown in Figure 1B).

Shell height (H) was measured by a traverse along the columellar axis from the apex to the outer edge of the reflected peristome, while the height of the body whorl (BW) was measured by traversing the same axis in the reverse direction until the crosshairs rested on the suture between the body whorl and the second whorl. The shell width (W) was measured by a traverse across the body whorl perpendicular to the body axis. Angulo-parietal width (APW) was measured by traversing across the tuber-

cle. The angular measurement (AXP) was obtained by positioning the vertical crosshair on the columellar axis with the origin overlying the columellar denticle, and then rotating the stage until the lower palatal lamella was parallel to the vertical crosshair. The lip-crest distance (LCD) was obtained by traversing the remounted specimen at right angles to the axis of the crest.

Climatic data for the sample localities were taken from the nearest reporting station of the United States Weather Bureau, for the period 1899–1938. The nine climatic parameters that were used correspond to average values for the nearest station, determined from published maps (Kincer, 1941). Their descriptions and abbreviations are given in Table 2. We inspected the relationship between each of the original morphometric parameters for the extant populations and the climatic variables corresponding to their sample localities by means of bivariate linear regression. However, only the two highest correlations are reported.

All statistical analyses were performed using the S-PLUS 2000 software package (MathSoft, 1999). Two primary analytical techniques were used. To examine the main dimensions of the multivariate structure of the morphometric data, for both extant and fossil populations, we used principal components analysis (Morrison, 1967; Gauch, 1982). This technique constructs linear combinations of the original measurements that maximally encompass the multivariate variation in the data. In particular, the first principal component accounts for the greatest variation in the data; the second component is orthogonal to the first component (i.e., is perpendicular to it and uncorrelated with it) and accounts for the second largest amount of variation; the third component is orthogonal to the first two and accounts for the next largest amount of variation; etc. The principal components provide a mathematically unique solution that effectively reduces the dimensionality of the original data. Typically, instead of having a large number of correlated measurements that together describe the morphological structure of an organism, the first few principal components often are sufficient to encompass most of the variation among the individuals in the several sampled populations. These synthetic variables thus represent uncorrelated aspects of organismal structure. Because two of the original morphological variables represented angular measurements, while the others were linear measures of the size of various aspects of the shell, our principal components analyses were based on the correlation matrix among the variables.

The principal components for the morphological structure of *G. procera* then were related to latitude, longitude, and the nine more specific climatic variables for the sample locations by using multiple linear regression techniques (Gauch, 1982; Sokal and Rohlf, 1995). Another

principal components analysis was undertaken with all four species, in order to examine possible changes in morphological structure over time. The final step in the analysis was to use the interpretation of the morphological principal component axes in terms of climate (via regression) to predict possible climatic conditions for the fossil populations on the basis of their physical structure, as indicated by their location in principal component space.

Results and Discussion

Univariate and bivariate analyses of extant populations

Table 3 presents the mean values for each measurement at each of the 31 sample localities of *G. procera*, as well as the mean annual values of each of the climatic variables at the nearest recording station. To investigate possible relationships between extant morphology and modern climatic conditions, we calculated the matrix of bivariate correlation coefficients, based on these mean values, between each of the seven structural parameters and each of the 11 climatic variables (Table 4). Linear regression analyses were performed on each of the 61 statistically significant correlations after correction for multiple comparisons (Sokal and Rohlf, 1995). However, because our primary focus is the relationship between the totality of morphological structure, which is a multivariate phenomenon, and possible climatic influences, here we present only the results of the two most significant bivariate correlations, viz., that between AXP and latitude ($r = 0.843$, $P < 0.001$) and that between LCD and latitude ($r = -0.819$, $P < 0.001$). Figure 2 shows the strong linear relationship between the mean values for the angle of the lower palatal lamella (AXP) and for the lip-crest distance (LCD) for each of the populations on which they were measured and the latitude of the sampling locality. As latitude, in turn, is highly correlated with certain specific climatic factors (e.g., TEMPAVE, $r = -0.974$; FFREE, $r = -0.943$; FIRSTKILL, $r = -0.873$; FROST, $r = 0.845$), this suggests the value of looking at total morphology and overall climate by multivariate methods.

Principal components analysis of morphological structure in extant populations

Principal components analysis of the morphological data, based on the matrix of correlations among the seven variates, was successful in capturing most of the variation among all 339 specimens (those with no missing values for all seven variates) in the first few principal components. Table 5 gives the "loadings," or composition, of each of the first three components in terms of their individual correlation coefficients with each of the original variables. Principal component 1 (PCA1), which accounted for 52.8 percent of the total variation in the data, loaded positively on all variables, especially the height, basal width, and total width of the shell; as is common in morphometric applications of

Table 3. Mean values for each locality for the morphometric and climatic variables, and for the scores on the first four principal components. All linear morphometric parameters were measured in hundredths of millimeters. Standard deviations of the morphometric variables are reported below each mean.

Code	H	W	WL	APW	AXP	LCD	BW	LAT	LONG	FROST	TEMPAVE	TEMPJL
A	236.9	104.4	5.5	13.9	85.3	16.6	125.8	38.26	78.00	9.0	56.0	76.0
	12.3	1.9	0.2	1.2	5.4	3.1	3.6					
B	254.4	111.1	5.6	16.5	87.3	18.4	132.3	38.57	76.08	8.0	57.0	76.0
	12.4	2.8	0.3	1.7	9.1	2.8	5.5					
C	243.0	109.3	5.6	14.8	68.5	16.3	126.5	35.97	83.92	9.0	57.5	76.0
	14.0	3.8	0.3	0.8	12.7	2.5	4.4					
D	261.7	110.1	5.7	15.4	77.3	14.3	135.0	39.10	84.51	9.5	54.5	75.5
	9.9	3.6	0.3	1.5	8.3	3.1	4.6					
E	255.0	108.9	5.6	15.0	74.8	14.0	131.6	38.38	88.06	10.0	56.0	77.5
	9.5	2.6	0.2	1.1	7.8	2.8	3.3					
F	252.0	108.0	5.6	14.0	74.1	14.9	129.9	38.62	90.19	15.0	56.0	77.5
	11.5	2.5	0.3	1.7	6.9	2.4	4.5					
G	252.7	109.7	5.8	13.5	60.9	18.4	126.9	33.27	86.71	2.5	64.0	80.5
	9.2	2.3	0.3	1.2	4.3	2.8	3.7					
H	243.4	102.4	5.7	14.0	76.1	16.1	123.7	38.91	99.88	16.0	54.0	79.0
	5.9	4.3	0.2	1.8	5.9	1.7	5.0					
I	238.8	101.7	5.6	13.9	71.7	15.1	122.1	38.91	99.33	16.0	54.0	79.0
	13.8	4.9	0.3	2.0	7.9	2.6	6.9					
J	240.2	102.3	5.7	15.8	79.0	16.0	119.2	36.73	100.52	10.0	56.0	80.0
	10.5	2.4	0.2	1.6	7.5	3.1	3.6					
K	235.7	98.3	5.7	15.2	74.3	18.3	119.6	36.73	100.52	10.0	56.0	80.0
	10.5	2.6	0.3	0.6	6.0	2.5	4.6					
L	259.4	107.7	5.9	16.3	61.9	20.7	131.0	34.85	98.46	7.5	61.5	81.5
	14.4	4.3	0.3	1.7	9.0	4.0	6.8					
M	241.1	103.9	5.7	14.2	68.2	15.7	124.8	33.60	98.69	6.5	63.0	82.0
	15.6	5.4	0.3	1.7	6.3	2.6	6.0					
N	282.9	120.2	6.0	17.1	60.9	25.0	146.0	29.95	98.66	2.5	68.0	84.0
	17.9	6.0	0.3	1.7	7.7	3.9	6.8					
O	245.5	107.8	5.7	14.1	62.0	18.2	125.5	32.34	87.20	2.0	65.5	81.0
	10.4	3.1	0.3	1.5	11.7	6.2	3.9					
P	234.5	104.1	5.5	14.6	86.6	18.0	123.2	38.89	77.03	11.0	54.0	75.5
	6.5	2.7	0.2	1.0	7.0	4.6	3.3					
Q	225.1	104.4	5.2	79.3	79.3			37.24	76.51	4.0	58.0	77.0
	11.5	2.3	0.2		7.9							
R	243.2	106.4	5.3	73.9	73.9			34.24	77.92	1.5	63.0	79.0
	6.2	2.5	0.1		7.4							
S	247.3	105.4	5.5	72.6	72.6			36.16	86.78	4.5	58.0	78.0
	10.5	2.8	0.2		10.2							
T	233.1	99.9	5.3	81.7	81.7			39.10	94.58	5.0	55.5	78.0
	13.5	3.9	0.2		11.7							
U	236.5	103.3	5.4	79.0	79.0			40.82	96.69	29.0	51.0	77.0
	7.0	2.5	0.2		9.1							
V	230.8	101.3	5.3	80.1	80.1			39.05	95.67	17.5	54.0	77.5
	12.0	3.3	0.2		10.1							
W	252.3	107.1	5.5	74.1	74.1			35.30	99.64	8.0	60.0	81.0
	17.6	4.1	0.3		14.4							
X	275.3	114.3	5.6	63.8	63.8			31.74	99.49	4.0	65.0	83.0
	6.5	3.5	0.1		4.3							
Y	262.0	110.4	5.6	58.2	58.2			35.21	101.83	6.0	57.5	78.0
	13.5	3.8	0.2		5.2							
Z	231.0	103.6	5.3	66.0	66.0			30.29	96.96	1.0	69.0	83.5
	10.4	1.7	0.3		7.8							
AA	237.5	102.7	5.4	70.3	70.3			30.29	96.96	1.0	69.0	83.5
	14.3	3.4	0.2		11.8							
AB	243.8	107.2	5.4	75.3	75.3			31.58	92.52	1.5	67.5	82.5
	8.7	3.7	0.2		8.9							
AC	244.5	107.1	5.5	74.0	74.0			34.73	87.82	3.5	61.0	80.0
	11.0	2.1	0.3		8.5							
AD	243.3	106.0	5.4	78.7	78.7			30.69	88.04	1.0	67.0	81.5
	15.7	5.6	0.2		7.5							
AE	258.6	107.7	5.7	75.8	75.8	15.3		39.77	86.16	20.0	52.5	75.0
	8.5	2.6	0.2		5.4	2.0						

Table 3. continued

Code	PRECSUM	PRECAVE	FFREE	LASTKILL	FIRSTKILL	CLOUDY	PCA1	PCA2	PCA3	PCA4
A	13.5	40.0	200.0	110.0	298.0	110.0	1.05	-0.70	-0.05	-0.13
B	13.0	40.0	200.0	100.0	307.0	110.0	-0.30	-1.30	0.59	-0.08
C	13.0	50.0	200.0	100.0	295.0	120.0	-0.27	0.41	0.21	-0.46
D	12.0	40.0	180.0	106.0	293.0	135.0	-0.95	-0.64	0.10	0.13
E	10.0	42.0	187.0	105.0	292.0	118.0	-0.45	-0.22	0.25	0.12
F	11.5	40.0	178.0	100.0	292.0	117.0	-0.28	-0.11	0.12	0.06
G	13.0	48.0	220.0	377.0	312.0	110.0	-1.14	0.77	-0.20	-0.33
H	10.0	24.0	170.0	117.0	285.0	75.0	0.41	-0.15	-0.83	0.02
I	10.0	24.0	170.0	117.0	285.0	75.0	0.67	0.37	-0.74	0.01
J	9.5	21.0	190.0	108.0	293.0	65.0	0.64	-0.33	-0.79	-0.08
K	9.5	21.0	190.0	108.0	293.0	65.0	1.03	0.19	-1.34	0.05
L	8.0	30.0	220.0	89.0	303.0	85.0	-1.33	0.58	-0.66	0.01
M	7.0	27.5	220.0	87.0	314.0	88.0	0.17	0.52	-0.65	-0.18
N	7.0	29.0	240.0	79.0	322.0	92.0	-3.55	0.02	0.63	-0.21
O	13.7	48.0	235.0	77.0	316.0	107.0	-0.62	0.84	-0.33	-0.42
P	13.0	40.0	200.0	100.0	103.0	110.0	1.14	-0.81	-0.18	-0.26
Q	16.0	45.0	220.0	95.0	309.0	105.0	1.79	0.17	0.60	-0.25
R	18.0	50.0	240.0	69.0	324.0	90.0	0.63	0.28	0.58	0.20
S	12.0	50.0	200.0	100.0	295.0	125.0	0.25	0.22	0.03	0.21
T	12.0	36.0	182.0	108.0	293.0	102.0	1.75	-0.13	-0.27	0.29
U	11.2	30.0	165.0	119.0	283.0	105.0	1.04	-0.13	-0.17	-0.02
V	12.0	34.0	180.0	112.0	288.0	100.0	1.78	0.06	0.07	0.17
W	8.0	27.0	220.0	95.0	303.0	80.0	-0.11	-0.04	0.16	0.24
X	6.5	25.0	230.0	384.0	314.0	85.0	-2.00	0.33	0.82	0.49
Y	7.0	20.0	180.0	74.0	329.0	55.0	-1.31	1.03	0.32	0.26
Z	8.0	31.0	260.0	79.0	324.0	95.0	1.16	1.15	0.24	-0.06
AA	8.0	31.0	260.0	79.0	324.0	95.0	0.97	0.67	-0.08	0.18
AB	13.0	55.0	240.0	71.0	316.0	105.0	0.42	0.05	0.46	0.03
AC	13.5	52.0	205.0	89.0	303.0	115.0	0.24	0.09	0.26	-0.04
AD	20.0	62.0	280.0	69.0	339.0	98.0	0.63	-0.19	0.31	0.11
AE	11.0	40.0	170.0	115.0	285.0	132.0	-0.61	-0.40	-0.14	0.24

principal components analysis, component 1 can be regarded as a general "size factor." The second principal component (PCA2), accounting for another 15.0 percent of the variation, involved a contrast between both APX, APW and WL (in the sense that loadings on the first two measures were high and negative, while the loading on WL was positive). The third component (PCA3) comprised an additional 11.7 percent of the variation, and consisted of a contrast between, on the one hand, LCD and the angulo-parietal width (APW), and on the other hand, height, the angular measurement (AXP), and whorl height (BW) and shell width (W). Thus, the first three principal components together account for nearly 80 percent of the variation in the morphological structure of *G. procera*, as captured in our seven measurements of 339 specimens from 31 localities across the range of the species.

Inspection of the location of the individual specimens in the three most important dimensions of principal components space (Figure 3) reveals that, as one would expect, the majority of individuals cluster tightly in a central region, corresponding to the average morphology of this snail. However, certain populations consistently deviate from this central tendency. For example, the *G. procera* population from Comfort, TX, clusters at the high end of PCA1, while the *G. procera* population from Dundee, TX clusters at the low end of PCA1 (see Figure 3A, letters N

and M, respectively). Since this component corresponds to a general size factor, snails from Comfort, TX are, on average, the largest in our dataset, while those from Dundee, TX are the smallest (as can be seen from the mean values given for all measurements in Table 3).

The *G. procera* population from Dailsville, MD (letter B) is distinct in lying near the low end of PCA2, corresponding, e.g., to high values of the angular measurement and angulo-parietal width. In contrast, the population from Bear Creek, AL (letter O) at the other extreme of the PCA2 spectrum, has low values for these measures (Table 3).

The plot of PCA2 versus PCA3 (Figure 3B) reiterates the distinctness of the two latter populations (letters B and O), as well as showing a continuum along PCA3 from the Cincinnati, OH population (letter D) at the low end to the Wichita Mountains, OK population (letter L) at the high end. This range corresponds to increasing values of, e.g., the ratio of LCD to height. This is not surprising, given the high correlation between shell height and other size-related parameters (in other words, shell height is an obvious and trivial surrogate for "size") and given the important correlation between LCD and climatic factors such as latitude (Figure 2B).

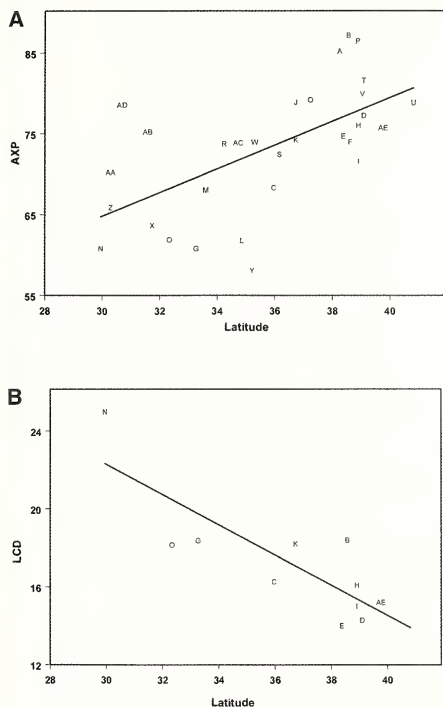
Relationships between multivariate morphological structure and climatic factors

Table 4. Pairwise correlation coefficients between morphometric parameters and climatic variables.

	H	W	WL	APW	AXP	LCD	BW
LAT	-0.483	-0.573	-0.771	-0.180	0.843	-0.819	-0.415
LONG	-0.124	-0.387	0.345	-0.161	-0.296	0.209	-0.204
FROST	-0.519	-0.659	-0.579	-0.259	0.594	-0.633	-0.472
TEMPAV	0.548	0.652	0.744	0.204	-0.774	0.796	0.480
TEMPJL	0.322	0.214	0.773	0.049	-0.728	0.760	0.207
PRECSUM	-0.374	-0.079	-0.474	-0.395	0.090	-0.391	-0.339
PRECAVE	0.120	0.437	-0.157	-0.140	-0.239	-0.142	0.157
FFREE	0.515	0.665	0.650	0.290	-0.678	0.776	0.475
LASTKILL	-0.051	0.004	0.104	-0.490	-0.342	-0.004	-0.174
FIRSTKILL	0.610	0.727	0.674	0.388	-0.541	0.799	0.565
CLOUDY	0.378	0.559	-0.101	0.133	0.031	-0.251	0.438

Table 5. Loadings of the first three principal components (PCA1–PCA3) on the morphometric measurements of *Gastrocopta procera*.

	PCA1	PCA2	PCA3
H	0.48	0.04	-0.28
W	0.45	-0.13	-0.18
WL	0.34	0.31	-0.17
APW	0.30	-0.54	0.27
AXP	-0.21	-0.76	-0.26
LCD	0.30	-0.05	0.82
BW	0.47	-0.12	-0.23
Standard deviation	1.92	1.02	0.90
Percent variance	52.77	14.99	11.67
Cumulative percent variance	52.77	67.76	79.43

**Figure 2.** Linear regression fits of the two strongest bivariate correlations for *Gastrocopta procera*. A, The increase of AXP, the angle of the lower palatal lamella, with latitude. B, The decrease of LCD, the lip-crest distance, with latitude. Symbols refer to the locality codes of Table 1.**Table 6.** Correlation coefficients between mean values for the specimens in a locality on each of the first three principal components and the climatic variables.

	PCA1	PCA2	PCA3
LAT	0.3451	-0.5792	-0.3055
LONG	-0.1785	0.4642	-0.4045
FROST	0.1853	-0.3708	-0.3653
TEMPAV	-0.2958	0.5246	0.3547
TEMPJL	-0.2692	0.5809	0.0160
PRECSUM	0.3965	-0.3052	0.2470
PRECAVE	0.1079	-0.1426	0.4463
FFREE	-0.1059	0.3636	0.3835
LASTKILL	-0.3206	0.1254	0.0834
FIRSTKILL	-0.2417	0.4382	0.2333
CLOUDY	-0.0027	-0.3624	0.3578

Table 6 gives the correlations between the mean values for each locality of each of the first three principal components and the values for each of the 11 climatic factors for each locality. It is clear, for example, that PCA1 is positively correlated most highly with total precipitation ($r = 0.397$) and with latitude ($r = 0.345$) and negatively correlated most highly with the date of the last killing spring frost ($r = -0.321$) and with average annual temperature ($r = -0.296$). This suggests that the general size of the shell of *G. procera* (PCA1) will be larger (and therefore the organism will attain larger sizes) at higher latitudes, which are typically colder and wetter within the continental United States. In this respect, *G. procera* appears to follow Bergman's rule.

The second principal component is most strongly positively correlated with the annual average and the midsummer temperature ($r = 0.525$ and $r = 0.581$, respectively) and negatively correlated ($r = -0.579$) with latitude (Table 6). Since higher latitudes correspond with lower temperatures over the biogeographic range of *G. procera*, these relationships imply that, based on our interpretation of PCA2 as determined primarily by a contrast between measurements of the aperture (APW and AXP) and WL,

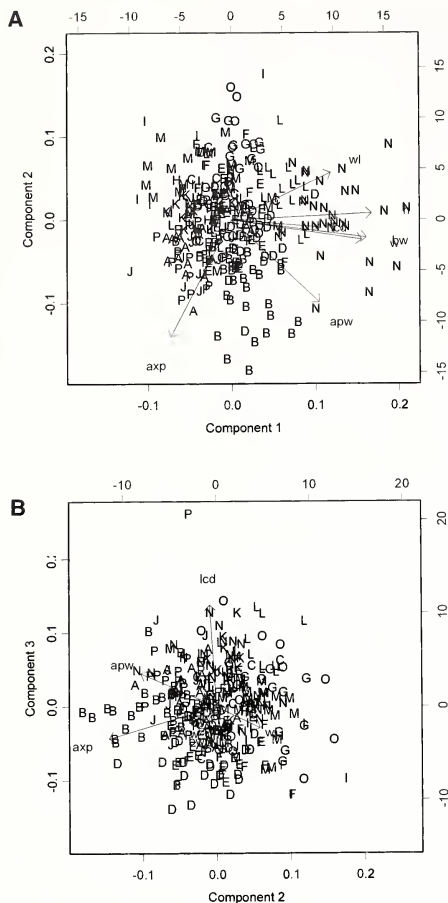


Figure 3. Location of specimens belonging to various populations of *Gastrocopta procera* (indicated with the locality codes of Table 1) in the morphometric space defined by the first three principal components based on the seven measurements of Table 2.

snails belonging to this species exhibit a relationship between climatic factors and functional morphology of the aperture that is not explained by general size alone.

The third principal component is positively correlated with average annual precipitation ($r = 0.446$) and negative-

Table 7. Results of multiple stepwise linear regression of the first two principal component of morphometric variables for *Gastrocopta procera* (PCA1) on the climatic variables.

Coefficients for PCA1:				
	Value	Std. error	t-value	Prob.(> t)
(Intercept)	-41.0362	10.7264	-3.8257	0.0007
LAT	0.5889	0.1642	3.5874	0.0014
LONG	0.0830	0.0322	2.5773	0.0160
PRECSUM	0.1531	0.0822	1.8633	0.0738
FFREE	0.0519	0.0176	2.9459	0.0067

Residual standard error: 0.9107 on 26 degrees of freedom

Multiple R-squared: 0.4823

F-statistic: 6.056 on 4 and 26 degrees of freedom (P-value is 0.001394)

Coefficients for PCA2:				
	Value	Std. error	t-value	Prob.(> t)
(Intercept)	3.2880	5.2289	0.6288	0.5348
LONG	0.0568	0.0207	2.7495	0.0105
TEMPAVE	0.1268	0.0498	2.5439	0.0170
TEMPJL	0.2009	0.1217	-1.6507	0.1104

Residual standard error: 0.4107 on 27 degrees of freedom

Multiple R-squared: 0.4850

F-statistic: 8.475 on 3 and 27 degrees of freedom (P-value is < 0.001)

ly correlated with longitude ($r = -0.405$). Our interpretation of PCA3 as a structural factor related to the relative size of the lip-crest distance (LCD) compared with the height of the shell suggests that snails with relatively large LCD are more likely to be found under the wetter conditions that are commonly found in the eastern part of the range of *G. procera*.

These and other piecemeal interpretations of the relationships between morphological structure and general climatic factors are intriguing. However, a more satisfactory approach is to find the best fit between values of morphological factors (in our case, principal components) and the entire set of climatic variables. Table 7 gives the results of the best multilinear regressions between each of the first three principal components and the 11 climatic variables. Thus, PCA1 is fit very well (multiple R -squared = -0.482 , $P < 0.01$) by a linear combination of latitude, longitude, total annual precipitation, and number of frost-free days, with the highest loadings on latitude and number of frost-free days. In other words, these four climatic variables have a highly significant predictive value for the major axis of morphological variation in extant populations of *G. procera*, an axis that accounts for more than half of the structural variation among 339 specimens sampled from 31 extant populations across the biogeographic range of the species.

Similarly, PCA2, the next most important general morphological factor can be predicted quite well (multiple R -squared = 0.485 , $P < 0.001$) by a linear combination of longitude and the two measures of average temperature (positively with respect to TEMPAVE for annual and negatively with respect to TEMPJL for July).

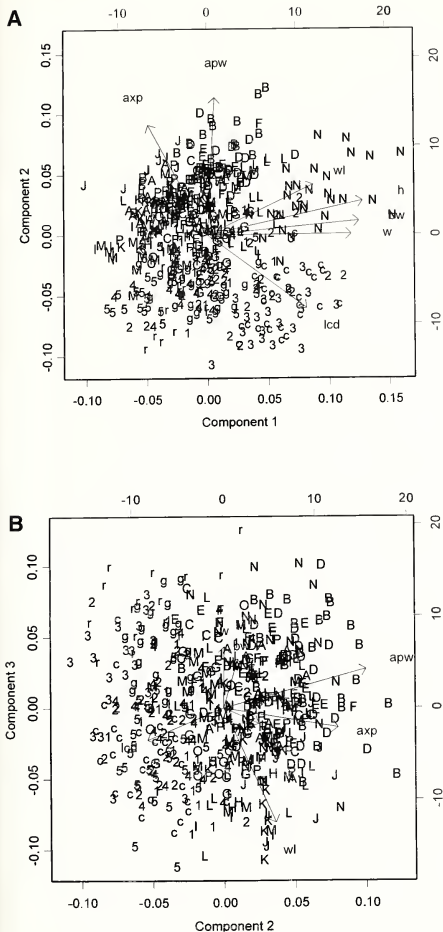


Figure 4. Location of specimens belonging to various populations of four species of *Gastrocopta* (indicated with the locality codes of Table 1) in the morphometric space defined by the first three principal components based on the seven measurements of Table 2. Populations of Holocene *G. procera* are denoted with uppercase letters; Pliocene *G. franzenae* populations are indicated with numerals; two Holocene *G. riograndensis* populations are denoted with the lowercase letter “r” and “g”, while a single Holocene population of *G. cristata* is denoted with the lowercase letter “c”

Table 8. Loadings of the first three principal components on the morphometric measurements of four *Gastrocopta* species.

	PCA1	PCA2	PCA3
H	0.51	0.17	-0.10
W	0.47	0.01	0.41
WL	0.35	0.25	-0.76
APW	0.02	0.68	0.26
APX	-0.20	0.55	-0.13
LCD	0.33	-0.37	-0.21
BW	0.50	0.07	0.33
Standard deviation	1.83	1.21	0.87
Percent variance	47.71	20.97	10.88
Cumulative percent variance	47.71	68.68	79.56

Morphological structure of fossil and congeneric populations

Data for 141 specimens belonging to five populations presumed to belong to the paleospecies *G. franzenae*, as well as 37 specimens from two populations of the Holocene species *G. riograndensis* and 29 specimens from one population of the Holocene species *G. cristata*, were combined with the 339 specimens of *G. procera* in a separate analysis. Figure 4 shows the disposition of both the fossil and extant specimens in the first three dimensions of *Gastrocopta* morphological space, and Table 8 gives the composition of the first three principal components, which together account for 80 percent of the total variation in the dataset of 546 *Gastrocopta* specimens. What is evident is that, while some of the fossil populations (e.g., population 4, from Seward County, KS) correspond to the size and shape of typical extant populations, some (population 5, from Meade County, KS) are located at the low end and some (population 3, from Oldham County, TX) are located at the high end of PCA1, which accounts for 48 percent of the total morphological variation. Since PCA1 again can be interpreted as a general size factor (although this time negatively correlated with the angular dimension), this implies that the fossil populations span the same range of sizes as modern populations.

Even more interesting, most of the fossil populations, as well as the other two extant species, lie at one end of the spectrum along PCA2 (Figure 4A), while none are located at the other end of this spectrum. PCA2 is primarily a contrast between APW and APX, on the one hand, and LCD, on the other (Table 8). This might be interpreted as a shift over evolutionary time in this organism from populations of snails with primarily one form of aperture morphology to the more typical morphology seen at the present time. However, since we have data only for a few fossil populations from one particular geographic region, such a conclusion is premature at this time.

What is most clear from the principal component analysis of all four *Gastrocopta* species is that the fossil species, *G. franzenae*, lies at one end of the morphological spectrum, in an area that overlaps with *G. riograndensis* and *G. cristata*, as well as some populations of *G. procera*. This supports the possibility that the evolution of morphological structure in this gastropod genus has been unidirectional over time, and that that direction is partially captured by PCA2. If so, *G. riograndensis* and *G. cristata* are more primitive than *G. procera*. This view would be strengthened by analyses of additional populations of fossil and extant species.

Gastrocopta riograndensis appears to occur in one restricted region of the morphological space defined by the first three principal components, while *G. cristata* lies in a different corner; the presumed ancestral species, *G. franzenae*, spans this region. However, only two populations of the first and one of the latter species were sampled, so this conclusion is tantalizing but not definitive. Clearly, more work on the systematics of these species is warranted.

Predicted climatic conditions for fossil populations

What the morphological distinctness of several of the fossil populations can tell us with some certainty are inferences about possible climatic conditions that were present at the time that the fossil populations were alive. These inferences rely on the assumption that the fossil populations belong either to the same biological cluster of species as the living ones (continuity of descent) or to species sufficiently similar in biology that they respond in the same way to major environmental factors.

Our results suggest that we may use the location of fossil populations in morphological space and the relationships between extant morphology and modern climatic conditions to predict aspects of paleoclimatic conditions. In particular, the location of the fossil populations at the high end of PCA2 (Figure 5) strongly suggests that they lived in conditions similar to those now present in the southern parts of the range of *G. procera*, corresponding to populations Y, Z, AA, and O (from Texas and Alabama; see Table 1). Unfortunately, there are no climatic inference data for the specific fossil localities sampled.

The correspondence between shell structural parameters and climatic variables can be used to predict the values of major climatic variables from the morphological principal components, using regression analysis. For example, Figure 6 and Table 9 illustrate the very good predictive ability of the first three principal components of morphology from *G. procera* in predicting the average annual temperature (TEMPAVE) and the average annual precipitation (PRECAVE) of the locations from which the populations were sampled. Assuming that we are correct in regarding all *Gastrocopta* species as responding,

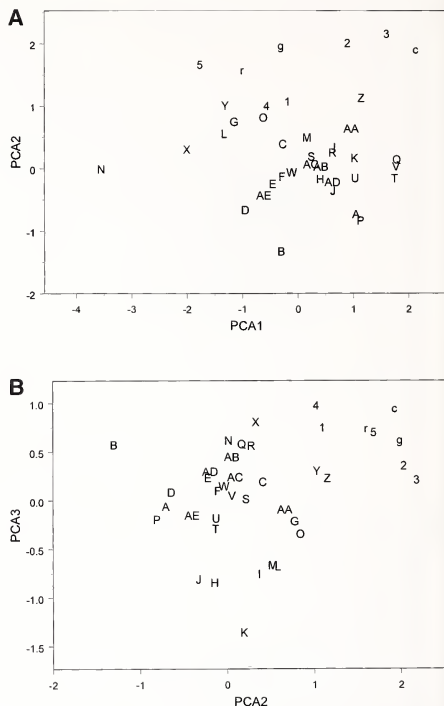


Figure 5. Location of the population means of all four species of *Gastrocopta* in the morphometric space defined by Holocene *G. procera* populations, as given in Figure 3. Abbreviations are as in Table 1 and Figure 4.

in their shell morphology, similarly to long-term climatic conditions, we can use these strong linear relationships in extant populations to predict plausible climatic conditions for the fossil populations of *G. franzenae*, *G. riograndensis*, and *G. cristata*. Table 10 gives the predicted values for these populations for these two variables, along with their 95 percent confidence limits. These results suggest, for example, that populations of the putative ancestral fossil species, *G. franzenae*, may have lived under conditions even warmer and wetter than those of present-day populations of the descendant species, *G. procera*, from Texas and Alabama.

These inferences from our morphological analyses could be tested further by more direct analyses of paleoclimate information for the fossil strata from which *G.*

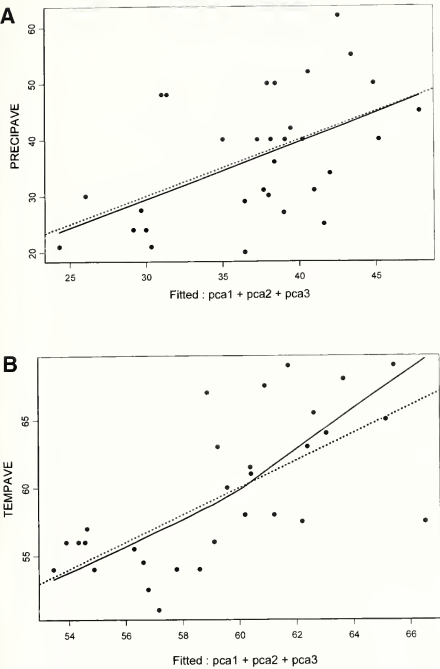


Figure 6. Predictions of average annual precipitation (A) and average annual temperature (B) based on the first three principal components of morphological structure in *Gastrocopta procera*. The dotted lines are the best linear regression fits, while the solid lines are the best polynomial fits.

franzeneae was sampled. The general approach of this paper illustrates the potential value of using morphology in the reconstruction of paleoclimatic conditions when other data might be unavailable.

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Table 9. Regression coefficients for predicting average annual precipitation (PRECAVE) and average annual temperature (TEMPAVE) from the first three principal components of morphological structure in *Gastrocopta procera*.

Coefficients for PRECAVE:				
	Value	Std. error	t-value	Pr(> t)
(Intercept)	37.3323	1.8593	20.0782	0.0000
PCA1	2.2548	1.6589	1.3592	0.1853
PCA2	-1.4768	3.4748	-0.4250	0.6742
PCA3	11.2385	3.8549	2.9154	0.0071
Residual standard error: 10.17 on 27 degrees of freedom				
Multiple R-squared: 0.2611				
F-statistic: 3.18 on 3 and 27 degrees of freedom (P-value is 0.03993)				
Coefficients for TEMPAVE:				
	Value	Std. error	t-value	Pr(> t)
(Intercept)	59.0760	0.7627	77.4578	0.0000
PCA1	-0.5801	0.6805	-0.8525	0.4014
PCA2	5.2831	1.4253	3.7066	0.0010
PCA3	3.8412	1.5812	2.4292	0.0221
Residual standard error: 4.173 on 27 degrees of freedom				
Multiple R-squared: 0.449				
F-statistic: 7.333 on 3 and 27 degrees of freedom (P-value is < 0.001)				

Table 10. Predicted average annual precipitation (PRECAVE) and average annual temperature (TEMPAVE), and their standard deviations (Std.) and 95 percent confidence limits, for Pliocene populations of *Gastrocopta franzeneae* (codes 1–5), and Holocene populations of *G. riograndensis* (codes r and g) and *G. cristata* (code c).

PRECAVE:				
Code	Inches	Std.	Lower	Upper
1	43.90	5.14	43.90	52.66
2	40.56	7.74	27.37	53.74
3	40.31	8.52	25.79	54.83
4	45.72	5.49	36.37	55.08
5	38.93	6.74	27.44	50.41
r	41.22	6.42	30.29	52.15
g	40.89	7.48	28.15	53.63
c	50.14	9.52	33.92	66.35
TEMPAV:				
Code	°F	Std.	Lower	Upper
1	67.92	2.11	64.33	71.51
2	70.72	3.18	65.31	76.13
3	70.54	3.50	64.58	76.49
4	68.65	2.25	64.81	72.49
5	71.77	2.77	67.06	76.49
r	71.03	2.63	66.54	75.51
g	72.22	3.07	67.00	77.45
c	71.74	3.91	65.09	78.39

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ANALYSIS OF DIATOM COMMUNITIES IN AN ACID-MINE-DRAINAGE-IMPACTED SUBWATERSHED IN SOUTHEASTERN OHIO 43

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T. WINGATE TODD: PIONEER OF MODERN AMERICAN PHYSICAL ANTHROPOLOGY

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ABSTRACT

T. Wingate Todd's role in the development of modern American physical anthropology was considerably more complex and profound than historians have previously recognized. A factor of the idiosyncrasies of his life and research, this relative neglect of Todd is symptomatic of a larger underappreciation of the field's professional and intellectual development in the early twentieth century. A complete examination of Todd's life reveals that he played a crucial role in the discipline's evolution. On a scholarly level, his peers recognized him as one of the most important men in the field and rarely challenged his voluminous written output, which comprised a significant portion of the period's literature. On a theoretical level, Todd led nearly all of his contemporaries in the eventual turn the field made away from the ethnic focus of its racist roots and the biological determinism of the eugenics movement. Furthermore, he anticipated the profound theoretical and methodological changes that eventually put physical anthropology on its present scientific footing. His research collections are the largest of their kind in the world, and still quite actively used by contemporary researchers. Many of Todd's publications from as early as the 1920s (especially those concerning age changes, growth, and development) are still considered standard works in a field that changed dramatically after his death. This attests to the fact that he was in many respects ahead of his time, and one of the most significant figures in the history of American physical anthropology.

Introduction and Historiography

In honor of its fiftieth anniversary on 11 and 12 December 1980, the American Association of Physical Anthropologists (AAPA) hosted a special symposium on the history of American physical anthropology at its birthplace of Charlottesville, Virginia. The papers presented at this symposium, combined with several others given at the plenary session of the fiftieth annual AAPA meeting in Detroit, became the bulk of the *American Journal of Physical Anthropology's* (AJPA) jubilee issue in 1981. This invaluable resource in the history of the field contains numerous articles on various topics and brief biographical sketches of several important early figures, including T. Wingate Todd (Figure 1). However, apart from this piece (Cobb, 1981), and an article by Frank Spencer on the rise of academic physical anthropology in the United States (Spencer, 1981), Todd appears virtually nowhere else in the volume. Even in the articles that pertain most directly to the areas Todd pioneered—a history of growth studies (Garn, 1981) and a history of studies in human plasticity (Hulse, 1981)—Todd's name is entirely absent, although the authors give well-deserved attention to his successors Wilton Krogman and William Greulich. Indeed, on a larger scale, most of the issue's various authors concentrate primarily or exclusively on developments of the post-1940 period. An important piece in

the literature on the history of the field, this issue of *AJPA* at the same time exemplifies the neglect of two significant aspects of American physical anthropology's past: first, neglect of the field's early twentieth-century history, and second, neglect of the role and work of T. Wingate Todd.

Physical anthropology completed the process of professionalization during this period, complete with its own journals, university-level academic programs, and scientific community. The field also began the transformation from its pseudo-scientific nineteenth-century past to a modern field of inquiry supported by truly scientific methods and theory. Standing among these changes was the life and work of Thomas Wingate Todd, M.B., Ch.B., F.R.C.S. Even within the field, Todd draws scant attention today compared to the other giants of his era. Columbia's Franz Boas, Harvard's Earnest Hooton, and the father of modern American physical anthropology, the Smithsonian's Ales Hrdlicka. In his time, however, Todd's peers recognized him as one of the most significant men in the discipline, and his published works arguably remain more durable than even those of Hrdlicka and Hooton. This paper strives to redress previous historical oversight of T. Wingate Todd, appraise his long-term scientific and professional significance, and discuss why he is not more widely recognized today.



Figure 1. T. Wingate Todd, photo taken late in life. (Photo courtesy of the Dittrick Museum of Medical History.)

In accordance with the minimal historical treatment of early twentieth-century physical anthropology, relatively little has been written on the major figures of the field from approximately 1900 to 1940 (with the major exception of those involved in the infamous Piltdown controversy, see Spencer, 1990, for example). Ales Hrdlicka, Arthur Keith, and Earnest Hooton have received some serious historical treatment, but beyond these men, researchers have paid considerably less attention to anyone else. Several factors have contributed to this relative oversight. The field was fairly small, commanding few professional workers and little institutional recognition. Increasingly overshadowed by the steady growth of cultural anthropological studies under Franz Boas and his students, institutional physical anthropology was also largely geographically limited to a Boston, New York, and Washington D. C. axis of cities on the East Coast. However, past historical neglect relative to earlier and later periods is ironic, as the transition of physical anthropology into its modern form occurred precisely at this time. Many people in addition to Hooton and Hrdlicka aided in this process, and Todd was a central figure throughout.

Apart from several short pieces of a popular nature (Gottlieb, 1982; Wood, 1983; Bailey, 1992; Jones-Kern and Latimer, 1996), published material on Todd falls into two fairly distinct groups. The first and most numerous of these are the obituaries, memorials, and remembrances written by his mentors, students,

and peers. A much smaller, second group consists of several descriptions of Todd and his activities written by people outside of his field. Although all make note of Todd's tremendous energy and the volume of his work, there are often sharp distinctions in tone between these groups regarding Todd's personality.

Works in the first group are generally glowing (even hagiographic) treatments of his life and work that are relatively indistinguishable in tone regardless of the time they were written (generally from 1939 to 1981). These notices and memorials not only bear witness to the tremendous amount of his work, but also its wide scope. Todd received obituaries in numerous journals in the fields of medicine, dentistry, anthropology, growth and development, anatomy, physiology, and surgery (see for example, Cobb, 1939; Keith, 1939a-c; Krogman, 1939a; Macklin, 1939; Shapiro, 1939). Some of these appeared many years after his death, highlighting items of his *oeuvre* that were of particular concern to the field in question (see, for example, Krogman, 1951; Cobb, 1959, 1981). All speak of the great importance of his work, especially the expansion of the Hamann-Todd collection and the Brush Foundation research. Although his personality is sometimes described using such adjectives as "forceful," there is rarely anything but appreciative comment made on his private or professional life.

The second group, representing items written from 1946 to 1997, often presents Todd in less flattering and/or more marginal

terms. Frederick Waite, a fellow faculty member of Todd's at Western Reserve, wrote a history of the Western Reserve Medical School in which he describes Todd in something less than the glowing manner reserved for almost all of the other professors and administrators he profiles. Waite accuses his colleague of possessing ill-defined, but unfavorable "certain characteristics" which manifested themselves in various ways, including questionable organizational maneuvers and "constant interference" (Waite, 1946, p. 389, 408). The few compliments paid to the man are either immediately mitigated or are left-handed swipes such as "[he] was an excellent teacher when he gave attention to this work" (Waite, 1946, p. 408). Perhaps the most unkind aspect of Waite's treatment of Todd, however, is one of omission. For a department chair, museum curator, prolific author, and anatomist of international reputation, Todd draws almost no attention from Waite past the disputed circumstances of his appointment, a bare and mixed appraisal of his tenure, and his death. By comparison, Waite gives other professors of lesser importance much more substantial and favorable treatment (see for example, Waite, 1946, p. 321, 346, 374).

Another less-than-flattering description of Todd is found in Alice Smuts' 1985 article on the National Research Council's Child Development Committee, on which Todd served as a member and (briefly) chairman. In this treatment, Smuts portrays Todd as an autocratic and unyielding leader who attempted to bend the Committee away from its traditional mission toward his own research goals. Using the correspondence and minutes of the Committee as her primary evidence, Smuts describes Todd as a person of great talent, but also of puzzling personality and questionable motivations (Smuts, 1985).

Elazar Barkan's *Retreat of Scientific Racism* has a fairly sizable section devoted to American physical anthropology during the early part of the twentieth century, but Barkan only infrequently mentions Todd relative to such contemporaries as Ales Hrdlicka, Raymond Pearl, Earnest Hooton, Franz Boas, Clark Wissler, Charles Davenport, and Melville Herskovits. Furthermore, in the sparse attention Barkan pays to Todd, he is called "a moderate physical anthropologist, a mainliner if ever there was one" (Barkan, 1992, p. 73). It is unclear upon what evidence Barkan bases this contention, but his book nevertheless paints Todd as a conventionalist and marginal in the anthropological debate over race in the early 1900s.

Not all independent portrayals of Todd are negative, however. Human growth scholar J. M. Tanner, who in his book about the history of growth research devotes several pages to Todd, bestows a great deal of praise upon Todd and his importance to that area of study. Tanner's recognition of Todd is more tempered than those of some of his students, but is nonetheless generally glowing (Tanner, 1981, p. 320–323). Similarly, Frank Spencer's entry for Todd in the *Encyclopedia of Physical Anthropology* dispassionately credits Todd with several important and lasting contributions to physical anthropology. Although necessarily brief, Spencer's piece particularly emphasizes the significance of Todd's work with the Hamann-Todd osteological collection and his research on age changes in the pelvis (Spencer, 1997, p. 1038–1040).

Fewer than 20 in number, these works as a group present a mixed and much less-than-comprehensive portrait of Todd. Beyond several basics concerning his work ethic and competence, they vary widely on nearly every other aspect of his personality and significance. Part of the reason for this puzzling diversity of historical impression may be the fact that most of Todd's personal

correspondence was lost, and authors have thus based their work mostly on personal recollections or letters in other collections. However, a number of other factors also contribute to Todd's enigmatic historical presence, including strong personal opinions of various authors, failure to utilize all available information, deliberate focus on only a single aspect of Todd's career, or personal idiosyncrasies of Todd himself. Although indicative of an undue, more general neglect of physical anthropology's early twentieth-century history, the sparse, piecemeal, and occasionally biased nature of Todd's treatment in the historical literature is also unwarranted because it fails to reflect fully his vital and continuing importance to the field's history.

The following pages endeavor to redress some of these inadequacies by providing the first comprehensive published biography of Todd, and demonstrating the crucial role he played in American physical anthropology's early development. Recognized as one of the most significant people in the field by his peers, Todd was a pioneer of the discipline's early scholarly, theoretical, and methodological evolution in ways that even his admiring colleagues could not appreciate fully. In filling this lacuna in the literature, this piece also hopes to serve as one small step towards a fuller understanding of American physical anthropology in the early twentieth century by scholars of the early twenty-first century.

"The best young man in England": Todd's Early Life

"A future in the diseases of children": Todd's youth, 1885–1903

Thomas Wingate Todd was born in Sheffield, England on January 15, 1885, the son of the Reverend James Todd and Katherine Wingate Todd. The Reverend Todd, son of an engine driver, was born and raised in Scotland and was proud of his ancestors' resistance to the Episcopal Church (Cobb, 1959, p. 234; A. Todd, personal communication, 19 August 1996). He trained and practiced as a Scots Presbyterian minister, but later turned toward nonconformism and spent the rest of his working life as a Methodist minister (T. W. Todd, n.d.b). Katherine Wingate, a physical education teacher, was the daughter of a dry goods merchant in Leeds and the sister of Sir James Laughton Wingate, a member of the Royal Academy (A. Todd, personal communication, 19 August 1996). James Todd met Katherine Wingate while he was working in Leeds, and when the Wingate family moved to Manchester, he moved there as well (Cobb, 1959, p. 233; A. Todd, 1988, and personal communication, 19 August 1996). James and Katherine married in England, and Katherine dutifully became a Methodist herself. (The conversion was out of love, not conviction. She went back to the Presbyterian Church on her husband's death [A. Todd, personal communication, 8 June 1995]). James was a popular minister. Todd's Cheatham Hill congregation in Manchester once kept him for six years as pastor, which was explicitly against Methodist rules of pastoral rotation (D. Todd, personal communication, 9 September 1996). The marriage, which ended with James' death in 1919, produced four children: Thomas, Katherine, Ruth, and Gordon (A. Todd, personal communication, 19 August 1996).

For some of his early years, Thomas Wingate Todd was a sickly child, his local school education occasionally interrupted by his bouts with different diseases (Cobb, 1959, A. Todd, 1988, and personal communication, 8 June 1995). He became so ill in 1898 that his family sent him off to a farm in Old Dalby, Leicestershire, for a year to recuperate and build up his strength (A. Todd, 1988,

and personal communication, 8 June 1995). Despite these setbacks and a move with his family to and from Liverpool, Todd continued his elementary education under private tuition and was graduated in a timely fashion from Nottingham High School (T. W. Todd, n.d.a; Shapiro, 1939, p. 458; Cobb, 1959, p. 233).

Todd's upbringing and childhood experiences had numerous long-lasting influences on his personality and professional life. Many of these effects were directly attributable to his parents. For example, although born in England, Todd adopted the speech patterns of his family and spoke with a small Scottish "burr" his entire life—an accent that he would occasionally "turn on full" for effect in his lectures and speeches (Cobb, 1959, p. 233; A. Todd, personal communication, 8 June 1995). In a broader linguistic sense, his father also instilled in Todd a love and sense of importance of ancient languages. The minister's son thus acquired an ability in Latin, Greek, and Sanskrit that he never lost (Cobb, 1959, p. 233; A. Todd, personal communication, 8 June 1995).

His father's religious background also contributed significantly to Todd's adult personality and work. Early in his adult life he taught Sunday school, once (according to his own account) contriving to make the walls actually fall down while covering the book of Joshua (A. Todd, personal communication, 8 June 1995). The most obvious manifestations of these influences on his mature work were the Biblical references and allusions that abounded in his speeches and his writings. On a more subtle level, one of T. Wingate's peers cited the Reverend Todd's nonconformism as being at least partially responsible for an independent streak that exhibited itself in many ways during T. Wingate's career (Shapiro, 1939, p. 458; Cobb, 1959, p. 233). His father's nonconformism may have also contributed to Todd's own somewhat ecumenical nature—he visited several different churches during his adult life, both Protestant and Catholic. Although not a regular churchgoer, Todd was nevertheless a man of profound religious faith who also had the greatest respect for the faiths of others (Shapiro, 1939, p. 458; A. Todd, personal communication, 8 June 1995). Todd reflected his personal religious outlook not only in his public speeches and private correspondence, but also in his professional work. In places, his scholarly publications betray a sincere belief in a guided orderliness in the world and nature. Knowledge of this belief is crucial to understanding Todd's "orthogenic" (or "directed") view of evolution (Todd, n.d.b. 1933b; Keith, 1939a, p. 350).

Todd's childhood battles with sickness left their mark on him as well. During the prolonged period of ill health, family members began to refer to the young Thomas Todd as "poor Tom," a moniker he despised (A. Todd, personal communication, 8 June 1995). The full impact of these unhappy years on Todd's adult personality is uncertain, as Todd spoke little and wrote even less on the subject. However, it is possible to make some reasonable conjectures based on what little information he chose to divulge. For example, according to his son Arthur (personal communication, 8 June 1995), the reason he dropped "Thomas" and began to refer to himself as "T. Wingate" betokened the degree to which he detested everything associated with his childhood nickname. Perhaps more significantly, Todd also stated that at the beginning of his medical career "all of my attention was turned towards pediatrics and I thought Fate was making for me a future in Diseases of Children" (Todd, 1929c, p. 4). It is not unreasonable to assume that Todd's unhappy experience with childhood diseases played a large role in his initial choice of career, nor is

it illogical to surmise that this interest inspired at least some of his tremendous later efforts to assess and improve the growth, development, and health of children through his original longitudinal studies and the Bolton and Brush Inquiries that followed (see "Todd's final years" below) (Todd, 1930b, p. 5).

Todd's childhood sickness may also have played a role in the relatively mild and specific form of eugenics he adopted later in life. He was critical of extremists in the eugenics movement who insisted that it was "dysgenic" either to institute preventive pediatric medicine or to try to "conserve" children of "relatively feeble constitution." These extremists thought that such measures were contrary to the laws of natural selection and thus weakened humanity. To have taken such a position would have been very difficult, even hypocritical, for a former chronically sick child such as Todd. Rather, Todd's brand of eugenics placed supreme emphasis on measures to ensure the healthy development of "well-born" children through family planning and prophylactic nutrition and medical care. Todd viewed all other commonly-held eugenic ideas (for example, forced sterilization of the "feeble-minded") as crude and secondary measures to the growth of well children. In some ways, then, Todd's dismissal of the vocation he felt "Fate" held for him was a bit premature, and the legacy of his sickly youth inspired him toward what many consider his most significant work (Todd, 1930b, p. 4–8).

Among the other long-lasting influences of Todd's youth was the development of a voracious appetite for reading and a passionate love of literature. From an early age, Todd read well and widely, always scribbling useful or pleasing passages and anecdotes on the back covers of an extremely eclectic array of books (A. Todd, personal communication, 8 June 1995). He was quite well-versed in the Bible and the Greek and Roman classics, and sprinkled quotations and allusions to these liberally throughout his speeches and writings, both public and scholarly. His knowledge of literature extended far beyond the classical and Biblical canons, though. Todd's writings and speeches were rife with references to the works of British authors (e.g., Browning, Hardy, Ruskin, Wesley) as well as non-British (e.g., Emerson, Melville, Montaigne, Turgenev), past (e.g., Carlyle, Pepsy, Pope, Swift) and contemporary (e.g., A. Huxley, Russell, Sand, Wells), great (e.g., Dickens, Shakespeare, Tennyson, Twain) and less-than-great (e.g., Giordano Bruno, Jean de la Bruyere, John Evelyn, Kropotkin). (The names listed come from a sampling of about ten percent of Todd's work by the author.) In addition, countless folktales, proverbs, and jokes—often of Scottish origin—found their way into Todd's works for illustrative or humorous purposes (Cobb, 1959, p. 233; Gottlieb, 1982, p. 41).

Beyond the simple anecdote or allusion, Todd's love of literature was also evident in his writing style. Indeed, several of the items in the Todd bibliography were purely literary in nature. As a student and faculty member at Manchester University he was active in the expansion of the University Press, and contributed pieces to the *Medical Student Gazette* (e.g., T. W. Todd, 1910b–e). His professional writing, cited by many as being unusually clear and forceful for his time and profession, was nevertheless at times prone to the majestic phrase or the grandiloquent flourish (Krogman, 1939, p. 144; Macklin, 1939, p. 200; Shapiro, 1939, p. 460; Jones-Kern, 1997, p. 152). A perfectionist at everything he did, Todd labored extraordinarily hard on his writing and was unusually jealous of his work (Keith, 1939a, p. 350–351). When he worked with coauthors he was extremely blunt in his critiques of their writing, and would not send an item to press with his name appended if it did not meet his

standards (Keith, 1939a, p. 350–351; A. Todd, personal communication, 8 June 1995). Several incautious editors drew the full force of his wrath in their attempts to alter his prose, yet Todd phrased even the angriest condemnations of editorial butchery in an extremely erudite, menacingly polite style (Jones-Kern, 1997, appendix B). Perhaps it was because of his literary flair that he became an extremely popular public speaker, not just in Cleveland, but across the country (Keith, 1939a, p. 350–351; A. Todd, personal communication, 8 June 1995).

The final significant legacy of Todd's childhood was the development of his abiding and intense affection for natural history. From a very early age, creatures of all kinds fascinated Todd and he exhibited a keen interest in nature. He tremendously enjoyed the company of animals, and received significant exposure to them in his formative years, not just from his year on the farm, but from years of volunteering his help at the local zoo (T. W. Todd, 1912; A. Todd, personal communication, 8 June 1995 and 19 August 1996). This affection for animal life continued throughout his adult life, and people often brought him sick and injured animals that he cared for as tenderly as he did when the Manchester and Cleveland zoos asked him to do the same (T. W. Todd, 1912; A. Todd, personal communication, 8 June 1995). Todd's laboratory at Western Reserve University was a haven for numerous different creatures over the years, including a raccoon, rhesus monkeys, a chimpanzee, and alligators. Todd kept the last of these as a kind of crude burglar alarm: sounding like "souls ... come back from the dead," they proved to be an effective intruder deterrent for an erstwhile morgue (A. Todd, personal communication, 8 June 1995). One particular lab favorite of Todd's was a lame chimpanzee dubbed *Claudius* (betraying again his weakness for classical allusion). Todd used *Claudius* in his developmental studies of children—whenever the ape was not busy untying the shoelaces of all of the lab workers and visitors (Gottlieb, 1982, p. 41).

Apart from the numerous humorous anecdotes concerning his Western Reserve menagerie, Todd's childhood status as an animal-lover produced several significant influences on his professional career. One of his earliest scholarly papers was a treatise on his elephant dissections—the first to demonstrate that the pachyderms have no pleura (T. W. Todd, 1913; Cobb, 1981, p. 518). A long-time member of the Cleveland Museum of Natural History and the Cleveland Humane Society, Todd joined numerous professional and scholarly organizations over the course of his career, including the American Association of Mammalogists, the American Museum of Natural History, the Boston Society of Natural History, and the American Society of Naturalists, and had a corresponding membership in the Zoological Society of London (T. W. Todd, 1912). Todd's keen and abiding interest in animal life resulted in his becoming one of the last great comparative anatomists, in a tradition stretching back to the Scotsman John Hunter in the 1700s (Keith, 1939a, p. 352–353; Krogman, 1939c, p. 143; A. Todd, personal communication, 8 June 1995).

College and early professional career: 1902–1912

After high school, Todd enrolled at the Manchester University Medical School in October 1902 at the age of seventeen (T. W. Todd, 1912). He met with great academic success in college, and it was there that he began to exhibit the seemingly boundless enthusiasm and energy that characterized his professional career. Along the way to his M.B. and Ch.B. degrees he gained the reputation of being one of the most distinguished medical

students of his university's recent past (Shapiro, 1939, p. 458; Cobb, 1959, p. 233). His laurels included the Junior and Senior Platt Scholarships in Physiology; every prize and medal for which he competed in the fields of anatomy, physiology, and surgery; and first-class honors upon his graduation in 1907 (K.A. Olliver, personal communication, 19 July 1996). The school respected Todd's abilities so greatly that upon graduation it immediately offered him positions in anatomy, physiology, and medicine (Cobb, 1959, p. 233). Because his personal academic interest lay in anatomy and his clinical interest in surgery, Todd eventually accepted the post of demonstrator of anatomy at the University of Manchester the same year (T. W. Todd, 1912; Shapiro, 1939, p. 458). He soon proved himself more than equal to the task.

Todd had only been demonstrating anatomy for one year when A. H. Young, head of the anatomical department, suffered a debilitating and eventually mortal stroke. If Manchester had appointed a new man to the position at that time, the gravely ill Dr. Young and his wife would have had little significant income (Cobb, 1959, p. 233). For this reason, and as many would later say befitted his character, Todd shouldered nearly all of the teaching and administrative responsibilities of the department for the year while Young still officially headed the department until his death in 1909 (Keith, 1939a, p. 350; Cobb, 1981, p. 518). Although only 23 years of age, Todd was solely in charge of the anatomical department at one of England's major universities until the well-respected Dr. Grafton Elliot Smith replaced Young in October of 1909 (Keith, 1939a, p. 350; Shapiro, 1939, p. 458).

The arrival of Smith had profound personal and professional ramifications for Todd. Smith, an Australian, had just arrived from Cairo where he was conducting the classic Egyptian investigations that would later win him a knighthood. Smith conferred upon his new young colleague the considerable task of cataloging and arranging the substantial amount of skeletal material collected under the auspices of the Nubian Archaeological Survey (Cobb, 1959, p. 233). This duty, which Todd executed admirably, had several long-reaching effects. First, his friends later credited it with developing in him a long-lasting enthusiasm for researches on "men of antiquity," and physical anthropology in general. Todd wrote about or cited the ancient Egyptian knowledge he learned at Manchester for the rest of his life (Shapiro, 1939, p. 458; Cobb, 1959, p. 233). Second, Todd's work on Egyptian skeletons (as well as his teaching talents) won him the friendship and respect of G. Elliot Smith, an influential figure in British academic circles. Smith later wrote a glowing letter of recommendation for Todd when he applied for the chair of anatomy at Western Reserve University, and the two maintained a warm personal and professional relationship until Smith's death in 1938 (T. W. Todd, 1912). Third, his exemplary work on the Nubian collection was largely responsible for Todd's election as a Fellow of the Royal College of Surgeons in 1911 (Keith, 1939c, p. 115). Todd proudly attached the letters "F.R.C.S." to the end of his name in all writings for the rest of his life (T. W. Todd, 1938; A. Todd, personal communication, 8 June 1995). Last, and perhaps most significantly, Todd's Egyptian duties gave him extensive experience in the curation and cataloging of large quantities of skeletal material. He later used this skill to build what is probably his most important academic legacy: the Hamann-Todd osteological collection (Shapiro, 1939, p. 458; Cobb, 1959, p. 233; A. Todd, personal communication, 28 June 1995).

During his time at Manchester, Todd's responsibilities and experience grew considerably year by year. In 1908, Todd began

to conduct classes for the primary (and occasionally, the final) examination for both the Fellowship of the Royal College of Surgeons in England and the Royal College of Surgeons of Edinburgh. Also, starting in that year, he was put in charge of delivering all descriptive anatomy lectures to dental students. This marked the beginning of a lifelong professional association with problems of dental anatomy (T. W. Todd, 1912). However, despite his already formidable anatomical knowledge and increasing duties, Todd felt that he needed much greater experience in surgical and clinical work than could have been gained from working at hospitals during "vacations" (A. Todd, personal communication, 8 June 1995). Accordingly, in October 1909 he took a sabbatical from nearly all of his teaching duties to become the House Surgeon at the Manchester Royal Infirmary (T. W. Todd, 1912; Cobb, 1959, p. 233). He became so adept at clinical diagnosis during this period and afterward that for the rest of his life Todd could recognize in total strangers the telltale symptoms of previous maladies at a single glance (A. Todd, personal communication, 8 June 1995). The experience in clinical and surgical anatomy he acquired at the Royal Infirmary were extremely influential in Todd's professional development, providing data and inspiration for some of his earliest published works and equipping him with the clinical skills he used years later in numerous surgical and clinical journal articles (Cobb, 1959, p. 233; A. Todd, personal communication, 8 June 1995).

Although crucial to his scholarly growth, his sabbatical was short-lived. In March 1910 his replacement at Manchester took another job and the University called Todd back, this time with the title Lecturer in Anatomy; a precocious accomplishment for a 25-year-old (T. W. Todd, 1912; Keith, 1939a, p. 350). Never one to shy away from responsibility, he served in both his clinical and academic capacities concurrently until his year at the infirmary was complete that August. In his new post, Todd soon had the opportunity to draw on his recent hospital experience. Manchester not only named Todd its Tom Jones Surgical Research Scholar, but also made him responsible for developing, demonstrating, and teaching a new course in clinical anatomy for fifth-year students (T. W. Todd, 1912). His new course was such a success that Ancoats Hospital invited him to give courses of post-graduate instruction in clinical anatomy (T. W. Todd, 1912; Keith, 1939a, p. 350). These events in 1910 are significant because it was at about this time that colleagues first gave considerable attention to a characteristic that remained one of Todd's hallmarks: teaching skills. Todd's abundant educational abilities were already attracting the appreciative comments and admiration of his peers, and his reputation as a teacher continued to grow for the rest of his life (Keith, 1939a, p. 350; Cobb, 1959, p. 233). Even colleagues who disagreed with (or even disliked) him during his career would later concede that as a teacher he had few rivals (Waite, 1946, p. 408).

The year 1910 was significant in Todd's career for another reason. Despite the duties and stresses involved in holding two jobs and organizing the teaching of new courses, he found time to write a series of contributions for the *Manchester Medical Student Gazette*, including his first scholarly publication, "An attempt to organize the description of the muscles of the spinal column" (Todd, 1910a). These modest articles were the first of nearly 300 published pieces Todd wrote or cowrote over the next 28 years. While this list embraced book reviews, published speeches, obituaries, and works of a general literary bent, over 200 entries in the Todd bibliography were scholarly in nature, including four book-length works. An extremely eclectic assortment, Todd's

written oeuvre included numerous items outside his professional realm of anatomy. Todd wrote articles touching on the fields of history, archaeology, cultural anthropology, sociology, psychology, surgery, medicine, mammalogy, human paleontology, primatology, allergy, and nutrition over the course of his professional life, attesting to his continued broad interests and well-read nature. Even in anatomy, his works were quite diverse beyond his primary focus on the musculoskeletal system. Apart from numerous articles on skeletal anatomy, Todd's published anatomical works included: a standard work on the microscopic anatomy of a specialized system of the heart; many articles and a book on dental anatomy; several pieces and two books on the gastrointestinal system; numerous articles and a book on growth and development; a textbook chapter on the respiratory system; and various items on the skin, the eyes, the tonsil, osteology, the nervous, vascular, and endocrine systems; x-ray techniques, and laboratory and clinical methods. Taking into account such impediments to his research as his years of service in World War I and his duties as teacher, administrator, and member and officer of numerous professional organizations, his publication average of nearly one item per month is truly astonishing (Jones-Kern, 1997, appendix A).

Todd's burgeoning industry at writing during this time did not detract from his efforts toward his established and increasing professional responsibilities. His teaching duties expanded as he took on lectures in systematics to medical students and developed several new courses, including anatomy for art students and anatomy and neurology for psychology students (T. W. Todd, 1912; Shapiro, 1939, p. 458). At the same time, Todd developed a new curriculum for the diploma in dentistry, and aided in the establishment of an entirely new degree in dental science (T. W. Todd, 1912; Shapiro, 1939, p. 458). He was also the official internal examiner for both programs. In addition to these classroom duties, Todd, by 1912, had five senior students (one of whom was his brother Gordon) conducting research under his direction, and the Anatomical Society of Great Britain and Ireland named him as one of their councilors (T. W. Todd, 1912). In his less-than-copious free time, he also took on the duties of anatomist and consulting veterinary surgeon to the Belle Vue Zoological Gardens in Manchester in 1911, displaying his ongoing devotion to and interest in the biology of other species, even while he was building a career in the biology of humans (T. W. Todd, 1912; Macklin, 1939).

Although all these manifold responsibilities and enviable experiences in multiple areas together had a significant impact on his career, nothing during his three years as lecturer in anatomy at Manchester had a more profound impact on Todd's professional life than his acquaintance and friendship with Arthur Keith. Already a prominent figure in anatomy and anthropology when Todd met him, Keith soon became internationally famous (and much later, infamous) for his association with the "discovery" and description of "Piltdown Man." (Later proven to be a hoax, some historians have suggested its perpetrator to be none other than Keith himself. See, for example, Spencer, 1990, chapter 8). Todd frequently visited Keith's lab starting around 1910 while he was beginning the first of his many investigations into growth and development of humans and primates. Todd's enthusiasm and prowess immediately impressed his elder colleague, and a deep, mutually affectionate and respectful relationship between the two developed that lasted until Todd's death (Keith, 1950, p. 342-343). His admiration for Keith needs no further proof than the fact that Todd named his first-born son

after his mentor (A. Todd, personal communication, 8 June 1995). Keith's reciprocal sentiments toward Todd were evident not only in the glowing descriptions he afforded Todd in his autobiography, but also in the several tributes Keith wrote for British scholarly journals in 1939 (Keith, 1939a-c; 1950, p. 342-343). Counting the soon-to-be Sir Arthur among his friends and admirers paid tremendous professional dividends for Todd, and literally changed the course of his life in conjunction with events that were transpiring more than 4,000 miles away in Cleveland, Ohio.

The call to Cleveland: 1912

While T. Wingate Todd was growing from an unwell child into a bright young anatomist in England, medicine in the United States was also metamorphosing from a sickly profession into a robust and technically advanced science. At its lowest point in the 1800s, American medicine was discredited in the eyes of much of the public for numerous reasons, including the practices of countless quacks and incompetents, the poor reputation of many hospitals, and a generally-perceived inability of the profession to explain or treat most diseases effectively (Ackerknecht, 1982, p. 218-222; Starr, 1982, p. 30-60). Because of the public's low regard for mainstream medicine, numerous challenges arose to conventional medical practice at this time, including homeopathy, dietary therapy, and even the development of Christian Science (Walters, 1978, chapter 7; Starr, 1982, p. 30-60).

In order to combat the erosion of public esteem for their profession, physicians in the United States began to take steps toward bringing respectability back to medical practice. Banding together to found the American Medical Association, these doctors worked diligently to oust quacks and incompetents from their ranks by instituting or strengthening licensing requirements to practice medicine in the various states (Ackerknecht, 1982, p. 210-226; Starr, 1982, p. 79-144). A key component of the new licensing procedures was an emphasis on adequate medical training as a requirement for receiving one's license. Thus, over the course of the nineteenth century, the old apprentice or preceptorship system of medical education was supplanted by numerous medical schools that began to spring up throughout the United States (Walters, 1978, p. 154-156; Starr, 1982, p. 79-144). A semi-standardized curriculum of coursework developed at the same time, which included a strong anatomical component (Waite, 1946, p. 343-344).

While medical education in the United States was becoming standardized, Pasteur, Koch, and others in Europe were conducting their ground-breaking research of microbes. From the 1860s to the 1890s, scientists discovered microorganisms were the cause of numerous diseases, and doctors for the first time were able to cure, rather than merely treat the symptoms, of several dreaded afflictions (Ackerknecht, 1982, p. 175-185; Starr, 1982, p. 180-197). This, combined with the efforts toward improving licensing and education, did much to restore the credibility of the medical profession in the United States (Starr, 1982, p. 180-197; Walters, 1978, p. 154-156).

It was in this milieu of change and expansion that Carl August Hamann (Figure 2) trained and began to practice medicine. In many ways an American parallel of T. Wingate Todd, Hamann was graduated with the highest average from the University of Pennsylvania Medical School in 1890, and received prizes for his scholastic aptitude. Like Todd, he felt himself to be in need of greater surgical training, and chose from among the internships offered him on that basis. While Hamann was serving at the

German Hospital of Philadelphia in 1891, the chief house officer went to Europe to study and the institution appointed the young intern acting head resident. He drew considerable praise from the staff, trustees, and official hospital report for that year, both for his administrative skill and his compilation of all the surgical cases in hospital files. Named the resident surgeon in the Mary J. Drexel Children's Hospital in Philadelphia the following year, Hamann also taught private anatomy courses, became the Assistant Demonstrator of Anatomy for the University of Pennsylvania, and started his own private practice in the course of the next two years. Hamann was performing these duties when Western Reserve University called him to their faculty (Waite, 1930, p. 3-4; 1946, p. 488-489).

In 1893, the Western Reserve Medical School was enduring one of the most turbulent times in its history. On top of extremely divisive issues concerning finances, administration, and curriculum reform, five of the faculty bolted to join the staff of a rival institution immediately preceding the fall term (Waite, 1946, p. 346-347). Western Reserve immediately charged three of their faculty who were on their way to attend a medical convention with the duty of also finding a new anatomy instructor for the medical school. Colleagues from Boston, New York, Philadelphia, and Baltimore advised them to pursue Hamann, whom the University immediately asked to become acting professor of anatomy (Waite, 1946, p. 369-370). The next year, at age 26, Hamann became the youngest full professor in the institution's first 100 years (Waite, 1930, p. 4-5; Waite 1946, p. 488-489).

Over the next 20 years, Hamann became one of the most highly regarded men not just in the medical school, but in Cleveland as well, for his untiring and multifarious efforts. Immediately upon his arrival he began to work as a surgeon in the college dispensary, and City and Charity Hospitals appointed him to their staffs over the next four years. By 1911, Hamann was Cleveland's leading surgeon (Waite, 1930, p. 5-6; Waite, 1946, p. 488-489). As a faculty member, he was an outstanding teacher and developed and taught extremely popular courses in applied anatomy that demonstrated the breadth of his knowledge by combining descriptive, comparative, and human anatomy with embryology, physiology, pathology, surgical diagnosis, and clinical surgery (Waite, 1930, p. 5-6; Waite, 1946, p. 488-489). In addition to these responsibilities, Hamann also wanted to build an anatomical teaching museum. He began to collect, mount, and buy specimens of various human and non-human materials. These created the nucleus of what would become the Hamann-Todd collection. Considering all of his accomplishments in different areas, it is little wonder that Hamann earned the affectionate nickname of "The King" in Cleveland's medical community (Cobb, 1959, p. 233-234). When a professorship of applied anatomy and clinical surgery opened in 1911, Hamann was a natural and popular choice to fill this position (Waite, 1930, p. 5-6; Waite, 1946, p. 488-489).

Although Hamann could have continued his departmental responsibilities, he felt that a Chair of Anatomy should be able to give his full time to teaching and research and resigned his post, effective at the end of the school year. President Thwing immediately appointed him to chair a committee to find his own replacement. This was a major decision, as anatomy was one of the most important subjects in the medical curriculum. Nearly two years passed before the search committee reported, a large part of the delay being caused by the sudden resignation of Dean Millikin and the elevation of Hamann to the post (Cobb, 1959, p. 233-234). The choice Hamann and his committee finally made



Figure 2. Portrait of Carl August Hamann, who was instrumental in bringing Todd to Cleveland and in creating the Hamann-Todd osteological collection. (Photo courtesy of the Dittrick Museum of Medical History.)

reflected not only the new dean's own proclivities but also larger forces of medical education at the time. As a result of the advances in medical knowledge and education in the half century prior to 1912, anatomical instruction itself was changing in the United States. Its premier medical institution, Johns Hopkins Medical School, was setting new standards of excellence. In terms of research and quality of education, Johns Hopkins received wide recognition as the best in the country almost from its foundation in 1876. Among the first to institute the modern college curriculum, the Baltimore college's medical school also followed the lead of the great European medical institutions and aggressively pursued research in the burgeoning fields of microscopy and bacteriology, adopting the latest technical methods. The new emphases of its anatomical curriculum on microscopic biology and increasing specialization came at the expense of more traditional instruction in gross, practical, and comparative anatomy. Johns Hopkins' prestige and that of its alumni made its curriculum very influential on other colleges and universities, shaping medical education methods across the country. To Hamann and others, this change was not entirely for the better, and for his replacement he wanted to find a professor who shared his own broad interests and conservative anatomical philosophy (Keith, 1939a, p. 350–351; Cobb, 1959, p. 233–234).

To aid Hamann in this decision, President Thwing had also appointed J. J. R. MacLeod and Frederick Waite to the search committee. Some dispute exists as to what happened at this point. According to Frederick Waite, professor of histology and faculty secretary, MacLeod wished to bring another graduate from an English institution to fill the post. "Another member" of the committee visited "the leading American anatomists" to seek their opinions on the best man to hire, and "incidentally asked

their opinion of selecting some man from Great Britain." According to Waite these anatomists all advised against such a course of action. After several weeks spent considering some Americans and "a young man in an English university," the committee was unable to come to a unanimous decision. They sent a majority report to the president of Western Reserve, who accepted it "under the misapprehension that it was unanimous." President Thwing then immediately cabled an offer to Todd (Waite, 1946, p. 407).

While Waite does not mention any committee member other than MacLeod, the Faculty Minutes make it clear that "another member" was Waite. Waite refers to himself in the anonymous third person elsewhere as well (e.g., Waite, 1946, p. 389), and he maintained an intense dislike for Todd (evident not only from his book but from remembrances from former students and family) throughout Todd's residency in the United States (Cobb, 1959, p. 234; A. Todd, personal communication, 8 June 1995). Significantly, Waite does not give the name of the third member and chair of the committee, Hamann. Perhaps it was because the revered professor and dean was in favor of choosing the man Waite detested that he chose to keep Hamann's identity a secret (Western Reserve Medical School, 1912; A. Todd, personal communication, 8 June 1995).

Arthur Keith and Todd's students offer a somewhat different account of this matter. According to this version, Hamann felt that because most of the best young anatomists in the United States were products of Johns Hopkins, and because the English anatomists stood closer to his conceptions of the traditions of practical medicine, he should look overseas. Thus Dean Hamann wrote to MacLeod's friend Arthur Keith for the name of "the best young man in England" to fill the newly-endowed Howard Wilson Payne Chair of Anatomy at Western Reserve University. Keith unhesitatingly recommended Todd (Keith, 1939a, p. 350–351; A. Todd, personal communication, 8 June 1995). Todd jumped at the opportunity, collecting recommendations from fellow faculty members (including G. Elliot Smith) and the vice-chancellor of the University to send with his forcefully-worded application for the job (T. W. Todd, 1912). In his broad interests, anatomical and surgical skills, intelligence, experience, industry, and precocious accomplishments, Todd reflected the new Dean's own career and traditional anatomical philosophies. Hamann offered the 27-year-old Todd the job in the autumn of 1912 (Keith, 1939a, p. 350–351; Gottlieb, 1982, p. 39; Behrens, 1984, p. 1–3).

The truth of the matter lies in the Case Western Reserve archives and reveals that Waite was at best a poor historian and at worst a deliberate prevaricator. Some circumstantial evidence points to this conclusion as well: Waite's *History* was not entirely unbiased elsewhere, and the long-standing mutual dislike he shared with his colleague may have colored not only his portrayal of Todd (marginal and largely negative), but even his rival's hiring process. While Keith and Todd's students were probably not without bias, either, there is little reason to suspect that Keith lied about Hamann's letter of inquiry or his own response, which no longer exists. The official committee report no longer exists, but a detailed account of it remains in the medical-school faculty minutes. These minutes dispute Waite's account on several points.

According to the faculty minutes for 3 October 1912, the search committee had been gathering information by interview and correspondence since its appointment nearly two years earlier. Waite traveled across the United States during this time and MacLeod visited extensively in England for the six months prior

to the meeting. Waite's account of his travels differs significantly from his published remembrance of "incidentally" asking "leading American anatomists" about hiring a person from "Great Britain." Rather, the minutes state that "one of the fundamental questions" regarding the search was the efficacy of hiring someone "from continental Europe." Of the fourteen Americans Waite consulted and quoted in the minutes, only three were professors of anatomy. The rest were professors of histology and embryology (1), physiology (1), pathology (1), medicine (1), and zoology (3); medical-school deans (2); the director of *Concillium Bibliographicum*; and a person from the Carnegie Foundation. Furthermore, it is clear from their quoted comments that these men's reservations rested on a belief that the anatomist in question was to come from a non-English-speaking country. These comments include "Advise against any other than an English-speaking foreigner," "it is extremely hazardous to take a German, Swiss less so, and British less risky yet," and "it is unwise to import a German unto [*sic*] a professional chair in this country." Waite instead nominated no less than 21 American anatomists for the post, but after the application of a number of disqualifying criteria (no medical training, unreliable research, known ill-health, lack of interest, immaturity and inexperience, inability to "fit into local conditions," and "personal and racial characteristics"), only six remained. To winnow this list further, the committee weighed additional conditions, including age (preferably under 40), research excellence, organizational and administrative abilities, teaching skill and experience, experience as a hospital resident, and certainty that the candidate would accept the position if offered. After the committee made all of these considerations, it "unanimously and with the concurrence of the ex-officio members of the committee (President Thwing and Dean Millikin)" recommended T. Wingate Todd. Thwing chaired the meeting and could not possibly have been under any "misapprehension" of non-unanimity, nor can the dispute between Waite's published account and the faculty minutes be blamed on contrary prejudices of the minutes' author: Waite was faculty secretary and signed the minutes as approved and amended. Thus, Waite's personal account of the matter is misleading, biased, and contains numerous inaccuracies.

Although the University has lost most other documents surrounding the affair, one can make reasonable suppositions from secondary and circumstantial evidence to fill in the historical gaps. MacLeod was a friend of Arthur Keith's, and probably suggested that Hamann write to Keith for advice. Keith in turn recommended Todd. Todd's dazzling application, accompanied by the strong recommendation of such internationally respected men as Smith and Keith, impressed Hamann and MacLeod, who wanted someone trained in traditional anatomical methods anyway. Despite Waite's strong reservations, he was not in a position to block Hamann's choice, especially since President Thwing was more than happy to agree with the new dean's choice for his own replacement. If this was the way it happened, Waite's dislike of Todd may have started before they even met, and the affair may also help explain some later animosities between the two.

Whatever the circumstances of the job offer, there is no dispute over the fact that Todd enthusiastically accepted. His appointment to the Henry Wilson Payne Chair of Anatomy became official in October, with duties to commence as soon as he could arrive. For the next two months Todd set in order his personal affairs and responsibilities in England (Cobb, 1959, p. 234). His

impending departure so moved his peers at the Manchester School of Anatomy that they staged an elegant farewell dinner at the Midland Hotel. Chaired by G. Elliot Smith, the event included toasts to the King and to Todd following a dinner of *consommé crouste au pot and crème medicis, filet de turbot d'Antin, crouste en ris de veau Toulouse, along with contré filet piqué sauce Tyrolienne, pommes rissolées, and haricots verts maître d'hôtel*, salad, biscuits, *canapés*, and *petits fours* (Anonymous, 1912). The celebration was doubly appropriate for Todd. Less than a week earlier, probably in his father's Cheatham Hill church, Todd married Miss Eleanor Pearson of Manchester (A. Todd, personal communication, 8 June 1995; D. Todd, personal communication, 9 September 1996). True to his professional nature, an engrossing dissection made him late for his own wedding to "Nell" on November 9 (Gottlieb, 1982, p. 38; A. Todd, personal communication, 8 June 1995).

On the surface, the reasons behind Todd's acceptance of the job at Western Reserve are not entirely self-evident. It is abundantly clear that he loved his native country: he never relinquished his British citizenship, visited as often as he could, volunteered to serve the Commonwealth in World War I, and displayed his devotion to England in numerous other ways for the rest of his life. In addition, he was also only at the beginning of what would have been a promising career in England. His rapid professional advancement and the respect of powerful friends in British anatomical circles indicate that his stature would have only increased had he stayed in Great Britain.

However, there were several attractions of the American position that weighed heavily in Todd's decision. Although Western Reserve did not have the prestige of an eastern university, its medical school was on the rise and gaining significant respect in the American medical community. Abraham Flexner, who conducted the influential Carnegie Foundation for the Advancement of Teaching survey on medical education in the United States in 1909, expressed to Western Reserve's president that his medical school was second only to that of Johns Hopkins (Waite, 1946, p. 384). Moreover, there was both a precedent and a pull to America in the person of fellow Scotsman J. J. R. MacLeod. Western Reserve's Chair of Physiology, a good friend of Arthur Keith's, and later a Nobel laureate for his work on the pancreas, MacLeod urged Todd to follow him to the United States and accept the position (Keith, 1939a, p. 352–353; Cobb, 1959, p. 235). Perhaps the most important factor in Todd's decision, though, was the very nature of the post. Even at his accelerated career path, Todd hardly could have expected an offer for a full professorship in England—much less the Chair of a university department—for years to come. The opportunity afforded by the Western Reserve position to the energetic and ambitious young anatomist was too attractive to pass up, particularly if Todd thought it would be only a relatively short-term arrangement (Cobb, 1959, p. 235, states that the initial appointment was only to be for two years). Both Keith and Todd's son Arthur later suggested that he had planned to come back to England—perhaps when a similar position opened up at a British university—but that he got too caught up in the work and unique opportunities of his position that he didn't leave, even when offers of English posts eventually arose. Although Todd visited England several times in the following years, he resided in the United States for the rest of his life (T. W. Todd, 1921g; Keith, 1939a, p. 352–353; A. Todd, personal communication, 22 May 1995).

"A century of endeavor, inspiration, and good will": Todd's American Career

Todd's journey to the United States in 1912 marks a convenient chronological divide for his biographers: at 27, Todd was almost exactly midway through his relatively short life. Of greater historical importance, however, is the division this year marks in his professional and scholarly endeavors. His childhood, education, and early professional experience all had lasting significance on the course of his life and career, but that course would have been much different had he stayed in England. He had started down a path involving anatomy, clinical medicine, and surgery at Manchester, and was contemplating a career in the diseases of children when offered his American post. From that point on, the singular opportunities his Western Reserve position presented and the still-formative state of somatology in the United States allowed Todd to bend his considerable skill and efforts toward a uniquely American end—the development of modern American physical anthropology.

Early years in Cleveland: 1912–1919

Todd matured professionally over the course of his life in the United States, but the first few years he spent in Cleveland set the tone for the rest of his career. Although his most important professional work did not culminate until after World War I, he had firmly established his major research interests by the time of the Treaty of Versailles. It was during this period that Todd conducted his earliest work on the alimentary tract and the dentition of humans and other mammals, two areas he explored throughout the rest of his career. On a theoretical level, Todd's earliest years at Western Reserve marked both his first forays into the field of physical anthropology, and the professional development of what became the major theme of research for the rest of his career: the growth, development, and maturity of humans, particularly as recorded on the skeleton. Perhaps most significantly, this interval also marked the beginning of his contribution to what became his major material accomplishment, the massive expansion of the Hamann comparative anatomy collection into the world-renowned Hamann-Todd osteological assemblage. Apart from his scholarly endeavors, Todd's first years in Cleveland also revealed his idiosyncratic (some might say autocratic) administrative style and the professional problems it continued to cause for the rest of his life.

Todd's earliest research in Cleveland focused on some of the problems he had been working on in Manchester. He published several articles regarding the clinical cases he had examined during his hospital work, as well as some pieces on comparative anatomy based on his work at the Manchester and Cleveland zoos. In 1915, Todd published his first book, *The Clinical Anatomy of the Gastro-Intestinal Tract*. An assemblage of his own clinical work in this area and the work of others scattered throughout the periodical literature, the volume received a tepid review from *The Lancet*, commending Todd for gathering so much information into one text but chiding him for not digesting or sorting the data more carefully (Anonymous, 1915). Reviews were considerably more kind for his second book, *An Introduction to the Mammalian Dentition*, published in 1918. Dental journals complimented him on his comprehensive work, his "terse and lucid" prose (Anonymous, 1918), and stated that "no lecturer on Comparative Dental Anatomy can afford to do without it" (Anonymous, 1919). Todd continued to pursue research on the digestive tract and dental anatomy until his death.

Perhaps his most important research of this period focused on the condition known as "cervical rib," in which a vertebra of the human neck develops a riblike structure. According to Sir Arthur Keith, this may have been the first work ever to describe arterial changes that result from pressure applied to the sympathetic nerve supply (Keith, 1939b). It was also the first paper Todd authored on the subject of growth and developmental changes reflected in the skeleton, a topic that became Todd's major professional focus and on which he was to do his most significant research.

Todd's early work in Cleveland also included his first professional work in the field of physical anthropology. Soon after his arrival at Western Reserve, Todd began to incorporate this subject into his lectures and the curriculum. (Waite, the Western Reserve Medical school historian, contended that Todd brought the subject into instruction "to a degree that brought continued complaints from students" [Waite, 1946, p. 408].) This may have been true, but Waite's fairness in dealing with Todd has already been demonstrated to be suspect.) His first published works of a strictly physical anthropological nature were also his only published items on fossil man and human ancestors. In a series of seven articles published in the *Cleveland Medical Journal* between 1914 and 1915, Todd summarized the state of knowledge in the field to that point, infrequently adding his own cautious speculations (T. W. Todd, 1914a–e and 1915b–c). Although these articles were by no means groundbreaking or significant in the debate of the larger anthropological community, they are an early demonstration of the independent and dispassionate nature of his scientific thought. With gracious apologies, he contradicted the expert opinions of his dear friends and mentors G. Elliot Smith and Arthur Keith when he felt the fossils spoke to a different conclusion. Despite his intense and lifelong interest in fossils and human origins, the lectures he gave about them in the United States and abroad, and the increasing public and professional attention paid to the field throughout his life, Todd never published another article on the subject (A. Todd, personal communication, 28 June 1995).

The work of greatest long-term significance from Todd's first years in Cleveland, however, was his expansion of the osteological and anatomical collections begun in the 1890s by his predecessor, Dean Hamann. When Todd arrived in 1912, the museum included the H. K. Cushing collection of Rocky Mountain mammals and about 100 human skeletons. Over the course of the next 26 years, Todd immensely increased the size and scope of both the primate and human components of the aggregation. By the time of his death, this amounted to hundreds of primate skeletons—including a larger orangutan collection than the Smithsonian's, the largest chimpanzee assemblage on the continent, and an eighth of the world's gorilla osteological material. In addition to the wealth of skeletal material, its accompanying collection of radiographs, photographs, and drawings remains an invaluable resource for primate scholars (Johanson, 1982, p. 2–4).

Perhaps even more impressive than this contribution to the collection, though, was Todd's acquisition of more than 3,000 human skeletons from the contemporary American population. Todd built most of this assemblage from unclaimed bodies at the Cuyahoga County Morgue and city hospitals. Both Hamann and Roger Perkins (director of Cleveland's Division of Health and Western Reserve's professor of preventive health) had made Todd's way in this effort easier by helping to revise the anatomical laws of the State of Ohio (Bickel, 1959). According to Ohio Code Sections 1713.34–1713.42 and 1713.99, the superintendents of city hospitals, the Cleveland Workhouse, and local mortuaries had to

notify Todd of unclaimed bodies in their possession (Wood, 1983, p. 60). These institutions sent the bodies to the medical school where Todd and his assistants measured and photographed them and recorded any other vital statistics that were available (for example: age, country of origin, address). He and his staff then generally embalmed the corpses for dissection in anatomy classes. After the bodies had served their instructional uses, Todd and his lab workers macerated them, labeled each bone with its acquisition number, and stored them in army surplus pine ammunition boxes (Figure 3) on a series of shelves (T. W. Todd, 1923a, p. 274–275; Cobb, 1932, p. 38–41). (Unfortunately, and to the chagrin of the legions of researchers who examined the collection over the next 50 years, these boxes bore army-issued numbers that bore no relationship to the actual numbering of their contents [L. Jellema, personal communication, 8 October 1996]).

The tremendous scientific significance of this collection (now housed at the Cleveland Museum of Natural History) is not so much in its size, but in its accompanying set of personal information. Each individual entombed in the collection has a corresponding file that contains the anthropometric and demographic data taken from that person at death. These data include name, age, sex, ethnicity, cause of death, and more than 70 body measurements listed on a standardized form. In addition, stereoscopic pictures and radiographs made of the individual at the time of his or her curation are included in the file, along with the results of any autopsies or dissections performed (Johanson, 1982, p. 1–3). With this unique and very extensive set of accompanying data, the Hamann-Todd collection remains the largest of its kind in the world (B. Latimer, personal communication, 23 April 1994).

The foreshadowing nature of Todd's initial scholarly endeavors in Cleveland accompanied similar portents of his mature administrative style. Almost immediately upon taking his position as Chair of Anatomy, Todd set about restructuring the department as he thought fit. Among other things, he attempted to place the Laboratory of Histology and Embryology under the administrative and financial control of his own anatomy department. This was not an entirely unreasonable action, as only six years earlier during a consolidation of 20 "departments" in the medical school into seven "divisions," the school placed the lab in the anatomy division. However, implicit in the 1906 consolidation agreement was the understanding that the histology and embryology lab would be "autonomous" in its budget and administration as long as its current director remained at the school (a similar arrangement existed between the Laboratory of Experimental Medicine and the Division of Medicine). Todd apparently either did not understand the finer points of this arrangement or he understood them perfectly and thought they were in error, because he almost immediately began to lock horns with the lab's director, Frederick Waite. This rivalry continued until Todd's death (or even after, it could be argued, as Waite [1946, p. 389–390] got the last word in his book published eight years later).

Although the histology and embryology lab saga at Western Reserve University was a relatively insignificant event outside the small circle of people involved, this episode is an important indication of the commanding executive style that characterized Todd for the rest of his career, both within his own department and in organizations over which he presided. His lab nickname was "The Chief," reflective of his role as head of a well-defined hierarchy of personnel (Krogman, 1934; Cobb, 1959, p. 237).

Based largely on age and seniority, one's rank showed in the size of the belt cinching his or her lab coat. While Todd's thick, braided rope was of course the largest (Figure 4), subordinates wore increasingly thinner ropes or clotheslines down to the youngest assistant, who tied his lab coat with a piece of string (Gottlieb, 1982, p. 40; A. Todd, personal communication, 8 June 1995). Although a strict disciplinarian, Todd was not what people later called a micromanager. Former staff and lab workers later fondly remembered performing their duties and research largely on their own and in quiet, with Todd occasionally striding past with the words, "Carry on," much in the manner of the military officer that he became in World War I (Cobb, 1959, p. 237; A. Todd, personal communication, 8 June 1995).

In 1915, Todd moved his family from their first Cleveland apartment to a house down the street at 1029 Ashbury Avenue (A. Todd, personal communication, 8 June 1995). World War I had started the year before, and Todd followed the events with interest and concern, having almost become involved in the war before either England or France. In 1914, he had visited his friend and mentor Arthur Keith in England, pushing on to Belgium afterward. Days later, he made an unscheduled return to England, narrowly missing being caught in the middle of the German invasion (Keith, 1950, p. 372–373). Professors and students from the medical school started to participate in the gathering American mobilization as early as 1916, and soon after the United States joined the war in April 1917, Todd decided to do his part. Still a British subject, Todd joined the Commonwealth war effort as a captain in the Canadian army. After medical officer training in London, Ontario, in the summer of 1917, he returned to Western Reserve to teach the fall term. In winter, the Army assigned Todd to serve in the Medical Corps, 110th regiment, 64th and 65th batteries, as officer in charge of the Surgery Base Hospital, Military District #1, London, Ontario. Later in the war, he served overseas as a consultant at Kinnel Park Camp in Wales. His interest and experience with the problems of bone growth and healing made Todd a conservative surgeon regarding amputation, and contemporaries later credited him with having saved the limbs of many soldiers (Cobb, 1959, p. 235). Although he did not serve with American forces, Western Reserve granted Todd the same leave of absence for the duration of the war extended to American servicemen (Western Reserve Medical School, 1917a, 1917b, 1918a, 1918b; Todd, 1918a, 1918b). In January of 1919 the faculty executive committee ordered Todd back to his chair, and elected him to their ranks. He returned soon after (Western Reserve Medical School, 1919).

The World War I experience cast a long shadow both on Todd's professional and personal life. Even though he was very busy executing his military duties, Todd still found time to publish some articles and his mammalian dentition book, as well as conduct his most important research on the heart with another Allied doctor, O. Van der Stricht. Along with the three articles coauthored with Van der Stricht (two in French—Todd was fluent) (Van der Stricht and Todd, 1919, 1920a, 1920b), Todd later wrote a standard textbook chapter on the special systems of the heart based on this work (Todd, 1928a). Although the period was an exciting and personally productive experience that he survived physically intact, he did not escape unscathed emotionally. His younger brother Gordon, who had joined the British army, died in 1917 of a nutritional disorder while serving in South Africa. It would probably be overstating the importance of this unfortunate incident to say that it was a major inspiration in Todd's later work



Figure 3. Skeleton room, Western Reserve School of Medicine. The Hamann-Todd collection was already the largest of its kind by the mid-1920s, when this photo was taken. (Photo from *Methods and Problems of Medical Education*, Third series, Rockefeller Foundation, New York, courtesy of the Laboratory of Physical Anthropology, CMNH. Used by permission of the Rockefeller Foundation Archives.)

on nutritional factors in growth and development, but it is not unreasonable to suppose it played some role in his later interest in the subject. Eager to get back to his growing family (his son Donald was born in July 1918 and his daughter Eleanor Margaret ("Toby") came a year and a half later), Todd, upon his discharge in 1919, took his military experience, research, and memories with him and returned to his home and position in Cleveland (A. Todd, personal communication, 8 June 1995; D. Todd, personal communication, 9 September 1996).

Establishing reputations: 1919–1928

The immediate postwar years were ones of great activity for the medical school and Todd alike. The college grew in size and prestige, occupying larger and better-equipped facilities along the way. Todd used the opportunities provided by this phenomenon to expand the facilities and workforce at his disposal. At the same time, Todd was also amassing a larger reputation for himself in the local and anthropological communities. He became a maker of high-quality anthropometric instruments, joined numerous civic and professional organizations, made influential friends, and most importantly, produced a tremendous volume of high-quality scholarship that propelled him in a few years to the height of his profession. For much of this, Todd had the medical school and its resources to thank.

Western Reserve's medical college had continued to grow in both size and reputation since Todd's arrival in 1912. Two years before Todd's appointment, Western Reserve removed some of its local competition by allowing the troubled Ohio Wesleyan Medical School to consolidate with them, accepting both their students and their faculty. This marked the beginning of a period

of great change. Between 1910 and 1924, the institution adopted a new curriculum, added a fifth year to the program, and admitted women for the first time. In addition, with the exception of a small dip during and immediately after World War I, the student body steadily increased during this period. To deal with the ever-enlarging student population, the faculty more than doubled from 67 to 149. Although the college occupied new buildings as circumstances permitted, its increasingly outdated and cramped facilities at East Ninth and Superior in downtown Cleveland (Figure 5) and its growing reputation in both instruction and research made it clear that the medical school needed a new building. In 1923, the same year that Todd personally moved into a larger home (2657 Shaker Road in Cleveland Heights), his school made plans to do the same. Thanks to the benefaction of Cleveland industrialist Samuel Mather, Western Reserve Medical School built a \$2.5 million facility in 1923 and 1924, the largest single building yet occupied by a medical school in the United States (Waite, 1946 p. 387–428).

The new building (Figure 6, now Case-Western Reserve's Harland Goff Wood Building, located at 2109 Adelbert Road in the University Circle area) was a windfall for the academic ambitions of both Hamann and Todd. Over three times the size of the three buildings combined that it replaced (Waite, 1946, p. 426–427), the new structure was spacious enough for Todd to expand his increasingly impressive departmental library, his anatomy laboratory, and the new Hamann Museum of Comparative Anthropology and Anatomy to which the dean named Todd director in 1920. With the aid of Dean Hamann, planners devoted a large part of the first floor of the structure to the museum (Figures 7, 8). The "central feature of the laboratory" of



Figure 4. Photo of Todd at work, showing the thickly braided rope he used as a belt. Seniority in Todd's anatomy laboratory was reflected in the increasing size of rope (or string) used to cinch one's lab coat. (Photo courtesy of the Laboratory of Physical Anthropology, CMNH).

anatomy, this facility was a teaching museum intended to fulfill the ultimate educational goal of the collection's founders: to provide "a unique opportunity for investigation and teaching alike, so thoroughly interwoven that they cannot be separated" (T. W. Todd, 1925a, p. 1–6). The completion of the laboratory and museum in the new building meant that the anatomy students Todd mentored for the rest of his tenure at Western Reserve received a rare kind of opportunity unduplicated anywhere else in the United States (Cobb, 1959, p. 235; Behrents, 1984, p. 37). Although his nemesis Waite (1946, p. 425–429) implied later that Todd neglected to use the agreed-upon floor plan for his department at the expense of the good of his students, Idell Pyle (a former student and colleague of Todd's) contended the arrangement of the lab during Todd's tenure was one mutually agreed to by Todd and Dean Hamann (Pyle, 1979).

The students specifically drawn to Todd's laboratory, and the increased acceptance of graduate students and fellows to the

college in the mid-1920s, provided the professor with a stable of assistants to aid him in his research, and his scholarly productivity increased dramatically (Waite, 1946, p. 453–455). An extreme perfectionist, Todd expected only the highest-quality work from his laboratory assistants. No matter how close personally to Todd, if an assistant failed to produce up to the most stringent standards he or she could expect to receive a dressing-down from "The Chief" (Todd's son Arthur, who often worked in the lab with his father, attests to the fact that not even family was exempt from this treatment [personal communication, 8 June 1995]). Although the experience of such an episode was unpleasant, it was also a powerful incentive to work carefully. In return for their work and ego-bruises, his students received generous credit in the texts of his articles, or often writing credit if they could stand the extreme scrutiny and criticism that Todd invariably gave all of his coauthors (A. Todd, personal communication, 8 June 1995). Todd also kept his research staff intellectually stimulated by the weekly conferences he held with them in the departmental library, often also attended by visiting clinicians and other specialists who shared their experiences with the students (Cobb, 1981, p. 520). This crucible of research produced some of the leading physical anthropologists of the next generation, including Wilton Krogman and W. Montague Cobb.

Several of these Western Reserve products were female, something of an oddity in the field at the time. Todd boasted a long-standing interest and pride in his instruction and promotion of women in academe. He made a special point of mentioning his experience in the instruction of women in his 1912 application (before the school was coeducational), and promoted the careers of women whom he felt were well qualified, with varying degrees of success (T. W. Todd, 1912). There was still widespread prejudice against female instructors in American colleges, and even in his own school Todd repeatedly and unsuccessfully attempted to hire Ruth Sawtell (Wallis) (a well-recommended student of Franz Boas who later published in her own right) for an anthropology position (T. W. Todd, 1927b). Nevertheless, of the 28 women who authored or coauthored articles in the *American Journal of Physical Anthropology (AJPA)* during the years the Western Reserve lab contributed most heavily to the publication, 6 (21 percent) were students of Todd and these contributed 22 percent of the articles by women (Jones-Kern, 1997, p. 183–184).

With all of these increasing material and human resources at his disposal, Todd and his associates produced a large volume of high-quality tools and research during this period. Dissatisfied with the caliber of some of the anthropometric equipment available for purchase, Todd established a machine shop (Figure 9) to produce measuring instruments that met his stringent standards. The shop made several standard anthropometric devices, but also developed several of Todd's own design. One of these, the "Reserve Craniostat," Todd invented and later modified with research fellow B. Holly Broadbent to become the "Western Reserve Craniometer"—the standard piece of equipment of its kind to the present (Behrents, 1984, p. 5–20). Todd also invented and produced the "Western Reserve Headspanner" and the "Western Reserve Bone Density Gauge" at his small machine shop (Krogman, 1939a, p. 158, 173–177; 1951, p. 680–684). Although his primary goal in setting up the machine shop was to make tools for his own research, Todd also produced instruments for sale to other anthropologists, including Boas and Hrdlicka (Boas, 1925a, 1925b, 1926a–c; Hrdlicka, 1936a, 1936b). Todd's mechanical innovations in the field of anthropology also



Figure 5. "Old" medical-school building. Located in downtown Cleveland, this building served as the home of the Western Reserve Medical School from 1887 to 1924. (Photo courtesy of the Dittrick Museum of Medical History.)



Figure 6. "New" medical-school building. Located in the University Circle area, this was the largest medical-school building in the country when constructed in 1924. It continued to serve as home of Western Reserve's Medical School until 1949. (Photo from *Methods and Problems of Medical Education*, Third series, Rockefeller Foundation, New York, courtesy of the Laboratory of Physical Anthropology, CMNH. Used by permission of the Rockefeller Foundation Archives.)

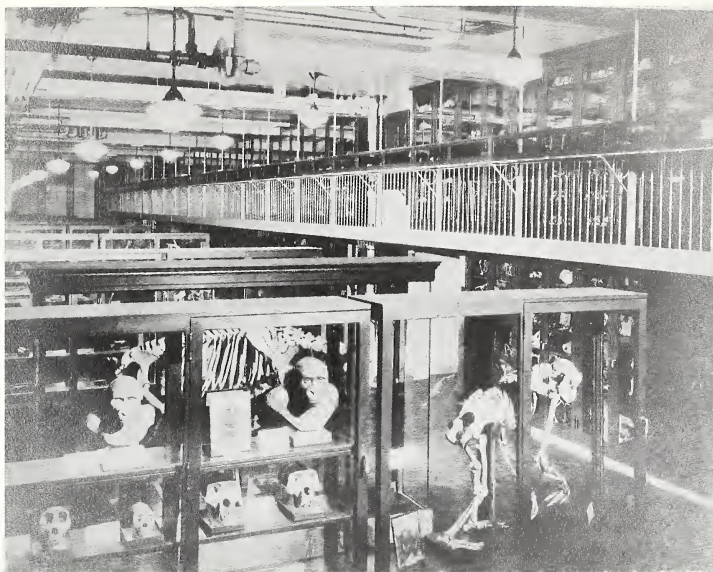


Figure 7. Hamann Museum of Comparative Anthropology and Anatomy, Western Reserve University. Taking up much of the first floor of the new medical-school building, it was designed to be the central feature of the laboratory. (Photo courtesy of the Dittrick Museum of Medical History.)

included experimentation with a Holorith machine in processing the large volume of measurements taken from the collection, perhaps the first use of computer technology in physical anthropology (Krogman, 1939a, p. 153–155; 1951, p. 679–687; L. Jellema, personal communication, 8 October 1996).

Using the new facilities and tools at his disposal, Todd published a flurry of research, much of which was of long-term significance. Some articles were continuations of his clinical studies from his early years in Cleveland and his service in World War I. These included yet another cervical rib paper and surgical pieces concerning pathologies of the shoulder, arm, and knee. His work on teeth continued with several articles in major dental journals. Some items concerned soft-tissue anatomy, including the heart and the tonsil, and a few dealt with the skeleton of non-human mammals. The first several of what would later be a large number of articles on the gastrointestinal tract also appeared late in this period. However, most of the papers produced during this time made extensive use of the rapidly expanding osteological collection and focused on anthropological methodology, race, growth and development, or some combination of these three topics (Krogman, 1939a, 1951; Jones-Kern, 1997, appendix A).

Among the methodological papers of this period were a number that dealt with the procedures and problems involved in amassing a large skeletal sample from cadavers. These included articles on measurement techniques and the effects of drying, mummification, and maceration on the skeleton. Although methodological papers rarely have great long-term scientific significance, the group of Todd's papers that deal with the measurement of cranial

capacity were quite important in the development of physical anthropology because they called into question some of the most basic, and mistaken, assumptions of the field's past. Todd's research, for example, challenged the efficacy of one of anthropology's oldest metrics—cranial capacity—and disproved the century-old anthropological contention that Black people have significantly smaller brains than White people. Todd's further work on the cranium also challenged long-held beliefs in racial differences in cranial shape, thickness, and suture closure patterns (Jones-Kern, 1997, chapters VIII–X).

The matter of cranial-suture closure, important as it was to racial issues, was also an important component in Todd's abiding interest in human growth and development. On this topic, Todd at this time wrote his papers on age changes in the pubic bone, arguably the most seminal and important articles of his career. In the skeletal collection Todd was assembling, he noticed that the morphology of the pubic symphysis (where the two pubic bones of the pelvis meet, separated by a plate of cartilage) changes in a standard fashion as humans grow older. After extensive examinations of hundreds of pelvises, Todd arrived at a set pattern of age-related changes by which an investigator may determine the approximate age of any individual based on his or her pelvis (T. W. Todd, 1920a, 1920b, 1921a–e, 1923a; Krogman, 1939a, p. 161–163). This discovery was of tremendous importance to the archaeological and forensic anthropological communities, as it provided an important tool in the physical description and identification of unknown skeletalized remains. With minor modifications, Todd's pubic-symphysis method of aging skeletons



Figure 8. Display Cases, Hamann Museum of Comparative Anthropology and Anatomy, Western Reserve University. The plentiful and readily accessible items in the Museum of Anatomy afforded medical students at Western Reserve a unique educational opportunity. (Photo from *Methods and Problems of Medical Education*, Third series, Rockefeller Foundation, New York, courtesy of the Laboratory of Physical Anthropology, CMNH. Used by permission of the Rockefeller Foundation Archives.)

has been in use to the present day, and his articles on the subject are still basic references, something extremely rare for physical-anthropology papers printed in the 1920s (Meindl et al., 1985).

These and other scholarly publications during this period greatly increased Todd's reputation locally, nationally, and internationally in a relatively short amount of time. For the period in the mid-1920s for which statistics are available, at least 66 Western Reserve professors published 140 articles based on primary research. Todd alone accounted for 21 (15 percent) of that number (Waite, 1946 p. 456). He also contributed a significant percentage of the articles published in the fledgling *American Journal of Physical Anthropology*. His meteoric rise in the anthropological community was such that while only in 1918 Ales Hrdlicka described Todd as an anatomist who "as far as his other strenuous duties will permit, is actively interested in Anthropology" (Hrdlicka, 1918, p. 392), by 1921 Todd was an associate editor of the *AJPA*, and by 1924 he wielded enough

clout to derail almost single-handedly Hrdlicka's plan to form the American Association of Physical Anthropology (Jones-Kern, 1997, chapter VIII). Todd's reputation extended beyond the American anthropological community. In 1921 the University of Ghent asked him to give a series of lectures in physical anthropology. Todd accepted the invitation, delivering his symposia in French (T. W. Todd, 1921f). Two years later, no less a personage than Howard Carter—the British archaeologist who had only the year before discovered the tomb of King Tutankhamen—called upon Todd's expertise in determining the age of skeletons. On the basis of the skull and leg bones Carter sent him, Todd concluded that the age of "King Tut" was 18 1/2 years at the time of his death, a determination still recognized as accurate (Gottlieb, 1982, p. 40; Williams, 2005, p. 7).

Todd's experience with Howard Carter illustrates an important dividend that resulted from his tireless efforts: the making of powerful friends and acquaintances in American academe. Already blessed with strong ties to such influential English-based scholars as G. Elliot Smith and Arthur Keith (who may have played some role in recommending him to Carter), Todd became increasingly well-connected after World War I in the anthropological and anatomical communities in the United States. During this period, he established professional associations with Charles Davenport, Earnest Hooton, Raymond Pearl, Robert Lowie, Alfred Kroeber, and a host of other major American anthropologists, anatomists, and biologists. Probably the two most important of these relationships were the ones Todd made with Ales Hrdlicka and Franz Boas.

Ales Hrdlicka was already the foremost physical anthropologist in the United States. From his base at the Smithsonian Institution, he had been indefatigably promoting the cause of physical anthropology since the beginning of the century. Hrdlicka never realized his dream of forming an American Institute of Physical Anthropology on the French model, but he achieved nearly every other goal he set for the development of the field before his death, largely by his own efforts. He established and edited the *AJPA*, and kept it alive in its early years, financing it largely out of his own pocket (Spencer, 1979, chapters 4–7). Todd had begun to correspond with Hrdlicka soon after he arrived in Cleveland, asking him for reprints and advice on organizing his department at Western Reserve (T. W. Todd, 1914f, 1914g, 1915d, 1917a, 1917b). Most of their infrequent pre-war correspondence was cursory in nature, but after the war their professional relationship blossomed. During the 1920s communication between the two increased dramatically, often averaging two or three letters a month, and its nature was mostly that of two mutually-respectful peers. Indeed, by the mid-to-late 1920s Hrdlicka had begun to defer to Todd in some matters (e.g., Hrdlicka, 1922). Although most evident in editorial matters, this deference manifested itself most significantly in Hrdlicka's offer of the AAPA's presidency to Todd in an abortive effort to launch the organization in 1924 (Hrdlicka, 1924a–c). Todd turned down the offer with equal deference (T. W. Todd, 1924b, 1924c; Jones-Kern, 1997, p. 273–289). Despite several strong disagreements they had over the years, Todd and Hrdlicka maintained an important professional association until Todd's death in 1938. One of the projects that Todd was overseeing at the time was a tribute to Hrdlicka in honor of his seventieth birthday (T. W. Todd, 1938e, 1938g).

In terms of the wider anthropological community, Todd's academic alliance with Franz Boas was more significant even than his relationship with Hrdlicka. Boas created the modern

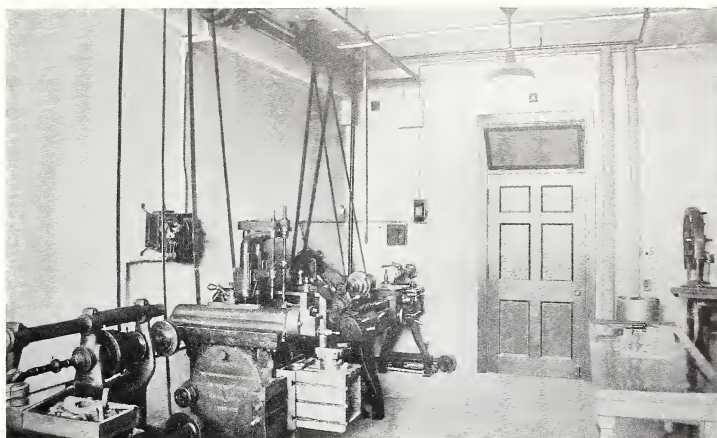


Figure 9. Machine Shop, Western Reserve Anatomy Laboratory. Todd produced high-quality measuring instruments here, including the “Western Reserve Craniometer” that is still the standard piece of equipment of its kind. (Photo from *Methods and Problems of Medical Education*, Third series, Rockefeller Foundation, New York, courtesy of the Laboratory of Physical Anthropology, CMNH. Used by permission of the Rockefeller Foundation Archives.)

conception of American anthropology in the late 1800s, and produced nearly all of its most significant early pioneers from his department at Columbia. Despite a brief loss of power and prestige for political reasons immediately after World War I, Boas was the most renowned and influential anthropologist in the United States, and arguably the world, by the 1920s. Boas conducted research in all fields of anthropology, but his important work in the physical anthropology of growth and development anticipated in nature and conclusions Todd's own. Sailing squarely against the tide of biological determinism that prevailed in the anthropology and eugenics of the early 1900s, Boas published his groundbreaking work on the physical anthropology of immigrants in 1912 that demonstrated the tremendous effects that environment and nutrition played in human growth and development (Hyatt, 1990, p. 26–85). Although most of his colleagues ignored or disputed this paper at the time, Boas found a sympathetic and supportive voice in the person of Todd. The two struck up a strong and mutually appreciative correspondence in the early 1920s, mostly focusing on the issues of physical anthropological technique and the promotion of Boasian ideas on environmentalism and race—ideas that Todd apparently almost entirely shared (T. W. Todd, 1923b, 1925b, 1926a; Boas 1925a, 1926f). Boas increasingly solicited Todd's aid in his projects and in the promotion of his students (Boas 1928, 1930, 1932, 1936, 1937a, 1937b), and Todd in return displayed an extremely deep level of respect for Boas in his writings that few of Todd's other peers claimed (T. W. Todd, 1927b, 1928c, 1929e, 1930d, 1933a, 1933c, 1934a, 1936a, 1937c).

The strength of his publications and the influence of professional admirers such as Hrdlicka and Boas resulted in Todd's rise to positions of prominence in professional and even national governmental advisory organizations. As early as 1919, the American Historical Association tapped him to lead a symposium

on the history of science at their Cleveland annual meeting (T. W. Todd, 1919b, 1938f). The following year, the American Association of Anatomists elected Todd both to the vice-presidency and to the council, a position he reprised in 1938. The Galton Society, formed in 1918, made Todd one of its earliest non-charter fellows in 1921. Although he was not one of its most active members, he maintained his fellowship in the organization for the rest of his life (T. W. Todd, 1938f). In 1921, Hrdlicka himself worked to get Todd appointed as Chairman of Section H (Anthropology) of the American Association for the Advancement of Science (T. W. Todd, 1922). Todd served again in the same capacity in 1933 (T. W. Todd, 1938f). In 1926, the Social Science Research Council named Todd to their Committee on Interracial Relations, and a year later the National Research Council appointed him to their Committee on Child Development (T. W. Todd, 1938f; Smuts, 1985, p. 111–117). The latter appointment had several significant consequences later on, but at the time was a natural outgrowth of his increasing expertise in that area. Many other posts and appointments would come his way in the years to follow (T. W. Todd, 1938f).

Despite his numerous above-mentioned academic and professional activities, Todd still found time to devote to non-research-based writing and civic affairs. Book reviews increasingly dotted his bibliography at this time (the first of which was on a volume by Keith, his old friend and mentor [T. W. Todd, 1919a]), as did articles for popular periodicals. He joined numerous local organizations, including the Cleveland Zoo, Museum of Natural History, Academy of Medicine, Medical Library Association, Museum of Art, Committee on Child Health and Protection, Health Council, Girls' Bureau, and the local chapter of the Humane Society (T. W. Todd, 1938f). Thanks to the work of Western Reserve University publicist Marie Kirkwood, Todd was increasingly in demand to give speeches and

lectures locally, and later nationally. He worked hard on these orations, which were usually entertaining and replete with numerous amusing anecdotes and literary references (Cobb, 1959, p. 236). By the 1930s he was appearing on Cleveland radio programs and had numerous articles devoted to his speeches and research in the Cleveland newspapers (e.g., T. W. Todd, n.d.a-c). While these various activities enhanced his local stature (and consequently, his university salary), they may have also had unfortunate repercussions in the jealousies they provoked among some of his university colleagues (A. Todd, personal communication, 8 June 1995). Because Todd's prolific efforts and sometimes difficult relationships with his professional peers are extremely important in understanding his work and legacy, a closer examination of Todd's personality is necessary before assessing his final years.

"Very obstinate if rubbed the wrong way, yet ... one of our most deserving, and hard workers": The Personality of T. Wingate Todd

The bewildering array of professional, popular, and civic activities and responsibilities assumed by Todd during his career begs a very simple question: How did he do it? Even with the aid of research assistants and the help of his peers, such an extraordinary amount of effort by one person is quite remarkable. To answer this question and gain insight into his style and personality, it is necessary to explore more thoroughly the personal side of Todd's life. The significance of such an investigation goes beyond the mere understanding of his astonishing productivity. A knowledge of some of the finer points of Todd's personality also illuminates some of his professional dealings and corrects some of the misinterpretations that subsequent investigators have made of his beliefs and actions. One must understand Todd's presence, work habits, home life, personal philosophies, and administrative and executive styles before completely assessing his life and career.

A large part of Todd's persona was rested in his formidable presence. Physically, he was a large man for his time. Nearly six feet in height and more than 200 pounds in weight, Todd cut a striking figure made more impressive by his upright and purposeful bearing (A. Todd, personal communication, 8 June 1995; M. Gaylord, personal communication, 22 July 1996). The most distinctive feature of his oval face was the pair of bushy, upturned eyebrows that matched the color of his much finer brown-black hair (M. Gaylord, personal communication, 22 July 1996). His appearance, coupled with dynamic and self-assured personality, made him a memorable and weighty force at any scientific gathering (Cobb, 1959, p. 236-237; 1981, p. 519-520).

However, the bulk of Todd's lofty scholarly stature resulted from his multifarious professional activities and prodigious, unimpeachable scientific output. To understand how Todd handled the volume of work and responsibilities he took on, one must first be acquainted with his attitudes toward work and time-management techniques. Todd was a paragon of the Protestant work ethic, and devoted most of his abnormally high number of waking hours to his duties. An ordinary day for Todd would be extraordinarily strenuous for most people. He woke up at four-thirty or five a.m., made his own breakfast, and went to the university where he worked until suppertime, bringing some business home with him on the trolley (Gottlieb, 1982, p. 40; M. Gaylord, personal communication, 26 May 1995; A. Todd, personal communication, 8 June 1995). After supper, he worked

on the projects he brought home for a while and went to bed at about eight-thirty. Arising again at eleven p.m., he toiled on his homework for a few more hours and then went back to bed again until five o'clock came around again (Gottlieb, 1982, p. 40; A. Todd, personal communication, 8 June and 28 June 1995). If he needed refreshment at some point during this cycle, he took a few minutes' nap and launched right back into his labors (Shapiro, 1939, p. 460). With minor adjustments and with the exception of times when he was ill, this was his daily routine for most of his professional life (A. Todd, personal communication, 8 June 1995).

This is not to say Todd's life was without diversions. He enjoyed reading his subscription to the *Manchester Guardian Weekly* and he spent most Sundays at home. A lover of the performing arts, Todd often attended theater productions or concerts by the Cleveland Orchestra. However, work was an omnipresent component even in his relaxation. On Saturdays he usually took the trolley to the medical school to catch up on work (although once in a great while he took the family out to a movie), and he occasionally went to the lab Sunday mornings as well (A. Todd, personal communication, 22 May and 8 June 1995, and 19 August 1996). Todd was known to pull out a briefcase during intermissions at the orchestra, but more often the restful atmosphere and music lulled him into an unscheduled nap (A. Todd, personal communication, 22 May 1995; Gottlieb, 1982, p. 40). Only "vacations" slowed his frenetic daily work pace, and even then only to more of a brisk walk. The family had an island retreat on Sugar Loaf Island near Muskoka, Ontario, where they would spend time hiking and boating. He was an avid sailor, having learned the hobby on the Clyde River in Scotland as a young man. However, even here Todd would bring work to do in the afternoons, his pounding on the typewriter in the bucolic surroundings earning him the nickname of "sapsucker" (A. Todd, personal communication, 22 May and 8 June 1995, and 19 August 1996; M. Gaylord, personal communication, 22 July 1996). Nearly every historical description of him, friendly and unfriendly alike, remarked upon his extreme industriousness (e.g., Keith, 1939a, p. 350; Shapiro, 1939, p. 460; Waite, 1946, p. 408; Cobb, 1959, p. 236; Cobb, 1981, p. 519-520; Gottlieb, 1982, p. 41).

Despite the extraordinary amount of time Todd devoted to his labors, his three children remember him as being a good father and family man. He made sure that supper times were sacred, as they were the only time of day that the entire family was together. Wednesdays he often came home early for family time and read interesting stories from the *Guardian* aloud. He was a dutiful son, bringing his mother over from England to live with the family after his father died. As a husband, "Hugheen" was affectionate to "Nellie, Dear," and rarely did either raise their voice in anger (A. Todd, personal communication, 8 June 1995 and 19 August 1996). His children remember "few spankings, few admonishments, and certainly no swearing or crude words" (M. Gaylord, personal communication, 22 July 1996). He was handy around the house, fixing and cleaning, and in the garden. As might be expected from a man with his childhood experiences, the health of his children was of great importance, and he made each of them take a dose of "black medicine" every night. A laxative potion of his own devising, it included belladonna (or as the children not-so-fondly remembered calling it, "deadly nightshade"), *nux vomica*, cascara, and some licorice flavoring to help it go down (A. Todd, personal communication, 8 June 1995 and 19 August 1996). His daughter Margaret remembers him being extremely patient and caring about everything from toilet-training accidents to the adolescent blues. In particular, she remembers an episode

when her mother, concerned about "Toby's" frequent habit of lying in bed daydreaming, asked her father if he thought something was wrong. He replied in an "astonishingly understanding" manner, "She's a teenager and this will pass" (M. Gaylord, personal communication, 22 July 1996). Even after his children left for college Todd kept in close contact, writing at least once a week. His affinity for and understanding of his own children extended on a larger scale to his dealings with the thousands involved in the Brush Inquiry, especially in the deep concern he felt for those who were not developing normally. His sons and daughter remember him as being a good whistler, singer, and artist as well (M. Gaylord, personal communication, 22 July 1996; A. Todd, personal communication, 19 August 1996).

More significantly, Todd's children also remember him as being remarkably socially color blind for his time and place. The ethnic and racial prejudices so pervasive in the United States of the 1920s and 1930s were not an issue in the Todd household (A. Todd, personal communication, 8 June 1995). Racial epithets joined profanity as forbidden vocabulary of the professor and his household, distinguishing Todd from other anti-racist pioneers in the field such as Raymond Pearl (A. Todd, personal communication, 8 June 1995; Jones-Kern, 1997, chapters X and XI). Unlike many of their peers, the Todds frequently hosted and entertained people from all ethnic backgrounds, including those of African and Asian descent. This relatively progressive behavior extended beyond the walls of the family's Cleveland Heights abode. Todd occasionally took his staff, including his African-American colleague W. Montague Cobb, to lunch at a local restaurant, blithely ignoring the pointed stares the party received from other diners (A. Todd, personal communication, 8 June and 28 June 1995). This and other evidence of Todd's racial egalitarianism disputes some portrayals of Todd in the historical literature (e.g., Barkan, 1992, p. 209–220).

The reminiscences of Todd's children also indicate the extent to which his vocation was a part of the family's life. In many ways, life in the Todd home was an extension of the father's laboratory work. Todd lost no opportunity to teach, and no one was exempt from study. His exacting lab performance standards, for example, also applied to his children. All of them were expected to get As at school; any other mark was "not a grade." He brought his sons into the lab to help him conduct his research from their pre-teen years on, and enrolled his daughter as a subject of the Brush Foundation studies, complete with the full regimen of radiographs and dispassionate descriptions of her physical state and mental abilities. Not one to make his children do something he would not, Todd made himself an object of study as well. On numerous occasions he served as his own guinea pig in digestive tract experiments, swallowing barium-laced meals or crackers larded with peanut butter and barium sulfate and having fluoroscopes made of their peristaltic progress (A. Todd, personal communication, 8 June 1995). Similarly, he presented fluoroscopes of his spastic colon as a visual illustration for a lecture presented to a national convention of graduate medical students (T. W. Todd, 1927a). The integration of Todd's home and work life was particularly noticeable on those occasions when the household actually resembled a laboratory. For example, when the Cleveland Museum of Art lent him the Egyptian mummy of Senbi the scribe to study in the early 1920s, it occupied for more than a month the space immediately in front of the fireplace. Similarly, when it was time to spay the family fox terrier, he brought his children down to the basement, opened the ironing board, anesthetized the dog, and performed the operation on her

while describing the process (an educational experience in more ways than one, it was about this time that his son Arthur began to suspect that he did not want to follow his father into the medical profession). Todd's infectious work habits and the premium he put on the acquisition of knowledge meant life in the Todd home was a beehive of activity and study (A. Todd, personal communication, 8 June 1995).

Because knowledge and research were so highly valued by Todd, he rarely let a unique opportunity to study pass him by even if it meant extreme inconvenience on his part. Once, while he was attending a function in Buffalo in the spring of 1924, Todd received an unsigned telegram asking him to come home immediately. Thinking it was a family emergency, he hurried home to find instead that the message came from the Cleveland Zoo. Nemo, one of the Zoo's elephants, had gone berserk after a prolonged illness and forced zoo custodians to shoot him dead (Chalfin, 1967; A. Todd, personal communication, 8 June 1995). They loaded the animal on a flatbed truck and deposited it in the alley behind the medical school. By the time Todd arrived, the body suffered extreme bloating from gasses created by the decomposition of undigested food. Todd wished to dissect the pachyderm—a task that eventually took several weeks—but decided first to release the gas build-up. He persuaded his anatomical colleague William Ingalls to thrust a knife into one side of the animal's stomach while Todd simultaneously did the same on the other side. Ingalls lost his nerve at the last moment, however. An explosive release ensued, resulting in an unpleasant shower of the creature's stomach contents mostly over Todd (A. Todd, personal communication, 8 June 1995; D. Todd, personal communication, 9 September 1996). The medical school at that time had no bathing facilities, so Todd cleaned himself off as best as he could in preparation to going home for a bath. Unfortunately, Todd never learned to drive a gasoline-powered car (despite the fact that he had driven an electric car before World War I), so he had to make his way home in a pre-washed state on the Shaker Rapid from Public Square to the Attleboro/Shaker stop. The ever-increasing distance put between him and the other passengers on the long trolley-ride home was a favorite family story; the fact that he undauntedly spent the next month climbing over and dissecting the carcass in the alley is an instructive example of the lengths to which Todd went to quench his chronic thirst for knowledge (Chalfin, 1967; A. Todd, personal communication, 8 June 1995 and 19 August 1996).

This story also illustrates another key component of Todd's persona and scientific philosophy: interdisciplinarianism. Although he was primarily a human anatomist and physical anthropologist, Todd displayed a keen interest in many other areas. Well—and widely—read, Todd was a renaissance man of the biological sciences and natural history, absorbing information from and contributing data to many different fields. This tendency had a number of significant manifestations in Todd's teaching, research, and professional activities.

In his teaching, Todd's interdisciplinarianism meant changes both to the curriculum and to instruction methods. While still at Manchester, Todd created courses in anatomy for art students and neurology for psychology students (Cobb, 1959, p. 233; 1981, p. 518). Almost as soon as he arrived in Cleveland, he added large physical anthropology and comparative anatomy components to the curriculum. The administration enhanced these additions by founding the Hamann Museum and making improvements to Todd's anatomy lab (Figure 10) in the medical school's new building (Cobb, 1936; 1959, p. 233, 235–236). Further moves

toward interdisciplinary integration included his gross anatomy course, in which he instructed dental students on the same basis as those in medicine, and his attempts to assume control of the embryology and physiology lab (Waite, 1946, p. 408). In addition, Todd used innovative techniques and equipment borrowed from other disciplines in his teaching methods. He pressed fluoroscope and x-ray machines into service along with slide and film projectors to enliven anatomy courses previously devoted almost exclusively to lecture and dissection (Krogman, 1939a, p. 149, 179-180). Occasionally, he even made his students study themselves by becoming subjects of Todd's digestive tract experiments. These too later became part of his anatomy courses (T. W. Todd, 1927a).

Todd's interdisciplinary nature is also abundantly evident in the research he conducted. Although Todd's primary focus was the human body, this concentration was only part of a deeper devotion to comparative anatomy and physiology. His proclivities in these areas went beyond simply contrasting human anatomy with humankind's nearest primate cousins. Todd also published scholarly articles on a number of other animals, including elephants, ungulates, and hyenas; and one of the final pieces of his groundbreaking series of pubic symphysis articles was a study of the guinea pig pelvis (e.g., T. W. Todd, 1913 and 1923c; Todd and Schweikher, 1933; Todd and Wharton, 1934; Todd and Todd, 1938). Even when it dealt solely with humans, Todd's research often involved much more than gross or skeletal anatomy. The radiographs and measurements taken from children participating in the Bolton-Brush studies were just two components of a comprehensive regimen of examinations into a child's total being. His staff inventoried the dental morphology, athletic skills, reflexes, and nervous system, psychological profile, intelligence, and talents of each Brush participant in an attempt to account for every major variable in child development (Behrents, 1984, p. 2-10). Thus, while the Bolton-Brush Inquiries resulted in a redefinition of normal skeletal growth in children, it also had a significant impact on other major fields as well. The psychological examinations carried out as part of the Brush studies, for example, culminated in a major revision of the Rorschach ink-blot test (Krogman, 1939a, p. 163-175; Cobb, 1959, p. 236-245). Perhaps even more significantly, the Bolton studies conducted groundbreaking dental and orthodontal research in the areas of craniofacial growth and tooth eruption that are still standard (Krogman, 1951, p. 679-687; Behrents, 1984, p. 2-10).

Professionally, Todd's interdisciplinary bent needs no further proof than the types of organizations he joined and the journals to which he contributed. Among the more than 60 professional groups and committees of which he was a member were associations devoted to mammalogy, genetics, medicine, natural history, art, history, dentistry, pediatrics, neurology, zoology, and public health (T. W. Todd, 1938f). His research also reflected these wide interests. He published pieces in dozens of different journals, including most of the major anatomical, medical, and physical-anthropological periodicals. However, much of his *oeuvre* consisted of pieces outside these fields. The publications represented in his bibliography (Jones-Kern, 1997, appendix A) include items in periodicals devoted to biology (*Comptes Rendus des Seances de la Société de Biologie*, *Human Biology*, *Proceedings of the Zoological Society of London*), the social sciences (*American Anthropologist*, *American Journal of Sociology*, *Bulletin et Memoires de la Société d'Anthropologie de Paris*, *Encyclopedia of the Social Sciences*, *Eugenics*, *Social Forces*), psychology

(*Journal of Comparative Psychology*, *Journal of Nervous and Mental Diseases*), history and archaeology (*American Historical Review*, *Annals of Medical History*, *Ohio Archaeological and Historical Quarterly*), dentistry (*Angle Orthodontist*, *Dental Cosmos*, *International Journal of Orthodontia*, *Oral Surgery*, and *Röntgenology*, *Journal of the American Dental Association*, *Journal of Dental Research*), pediatrics and child development (*Child Development* [also associate editor], *Growth* [also associate editor], *Journal of Diseases of Children*, *Journal of Pediatrics*), therapeutics (*American Journal of Roentgenology and Radium Therapy*, *Journal of Pharmacy and Experimental Therapeutics*), surgery (*Annals of Surgery*), nutrition (*Journal of the American Dietetic Association*, *Journal of Nutrition*), pathology (*American Journal of Pathology*, *Journal of Allergy*), and science in general (*Ohio Journal of Science*, *Science*, *Science Monthly*, *Scientific Monthly*, *Sigma Chi Quarterly*). Even *Progressive Education* and the *Journal of Home Economics* featured articles from Todd's versatile pen.

Todd's interdisciplinaryism had other significant professional effects, both in his conception of the field of physical anthropology and his long-term place in the field. As an anatomist in the Hunterian tradition and a physician who turned his attention to many different problems of human health, Todd disapproved of the increasing specialization and compartmentalization of the medical and anthropological fields as being largely detrimental to the pursuit of knowledge (T. W. Todd, 1924b). Along these lines, he bemoaned the exclusion of medicinal botany from the medical curriculum as well as the historic separation of the surgical and medical-pharmacological professions in his native England (T. W. Todd, 1937f). In America, Todd had several of his pieces rejected by anthropological journals because the editors felt they were not sufficiently anthropological in focus (T. W. Todd, 1934f; Spier, 1934a). Todd reiterated the theme of disciplinary inclusiveness frequently in his speeches and correspondence, and this philosophy played a large role in his opposition to the founding of the AAPA (Jones-Kern, 1997, chapter VIII).

In addition, the division of Todd's attention and resources toward his multifarious interests may have had an impact on his long-term recognition and influence in the physical-anthropological profession. Other major figures of the time such as Hrdlicka and Hooton devoted most of their published *oeuvre* to research in physical anthropology. Todd's publications, although of undeniable quality and arguably greater scientific value than those of his major colleagues, spanned a number of different topics and fields. Even within physical anthropology, much of Todd's work was of marginal interest by the standards of the day. He virtually ignored the growing focal topics of human origins and fossil man in his publications, and instead devoted the bulk of his research efforts to growth and development—an area that remained on the periphery of physical anthropology for decades to come (Garn, 1981, p. 521-525; Jones-Kern, 1997, chapter IX).

Apart from its impact on his contribution to the literature, Todd's devotion to interdisciplinaryism affected his long-term professional influence in another, more important way: his students. Hooton's tremendous significance to the field of physical anthropology was less a result of his published work (much of which is now dated) than it was the number of students his Harvard department turned out and their extraordinary role in shaping future generations of American physical anthropologists. Most of the major new university departments of physical anthropology created during the field's biggest boom after World

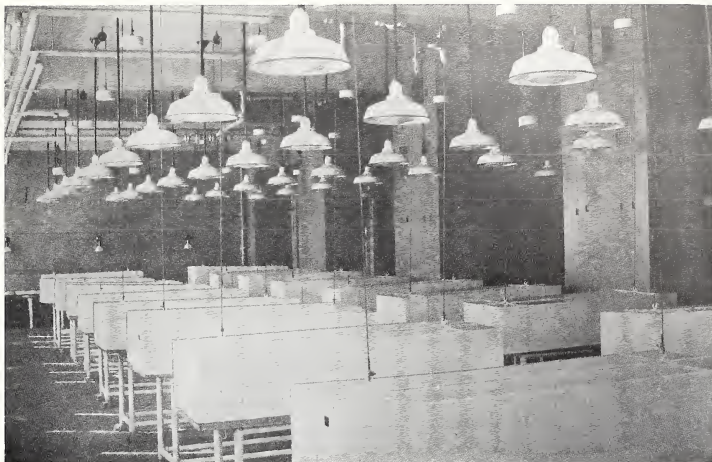


Figure 10. Dissection Room, Anatomy Laboratory, Western Reserve University. Many of the bodies that made their way into the Hamann-Todd collection were first dissected in this then state-of-the-art facility. (Photo from *Methods and Problems of Medical Education*, Third series, Rockefeller Foundation, New York, courtesy of the Laboratory of Physical Anthropology, CMNH. Used by permission of the Rockefeller Foundation Archives.)

War II formed around graduates of Hooton's prolific Harvard program (for example, Carleton Coon, Stanley Garn, William W. Howells, H. L. Shapiro, Sherwood Washburn), and thus Hooton disciples exerted a tremendous degree of influence on the course of the discipline for decades (Spencer, 1982b, p. 6–9). In contrast, Todd's graduate students—already limited in number due to institutional controls and his own tough standards—trained in several different primary disciplines (Krogman, 1939a, p. 176–177). Some of his most talented protégés (for example, B. Holly Broadbent, F. E. Randall, Theodore Zuck) pursued careers in fields such as dentistry and medicine. Thus, the number who went on to take an active part in physical anthropology's post-war expansion was smaller still (Cobb, 1936, p. 8–14; 1956, p. 83–89; 1959, p. 236–237; 1981, p. 519–520). As important as Cobb or Krogman may have been, they could not match the influence of Hooton's numerous academic offspring.

If interdisciplinarianism was one key component of Todd's scientific philosophy, an unusual freedom from bias was the other. The standard physical-anthropological practice before Todd's time was to collect facts that fit one's preconceived ideas, usually regarding race and ethnicity. Although Broca and his French colleagues provide the salient examples of this custom, most American researchers followed the same practice. Todd's contemporaries Robert Bennett Bean and Charles Davenport were the most extreme exemplars of this mindset, but even more moderate anthropologists such as Hrdlicka and Hooton firmly believed in such preconceived notions as racial hierarchies (Gould, 1981, chapters 2–3; Barkan, 1992, p. 95–108). In contrast, Todd usually built his general scientific principles on the results of his experiments and observations, even if it meant abandoning his earlier assumptions. To avoid the taint of bias in most of his major work, Todd first amassed great quantities of data, from

which he drew only the most conservative and incontrovertible conclusions. It is true that Todd's approach fell somewhat short of modern scientific methods, and he held on to certain erroneous assumptions (for example, the typological orientation of his profession [Jones-Kern, 1997, p. 353–373]). However, Todd was nearly alone among his peers in the extent to which he allowed the data to shape his beliefs. On more than one occasion he confessed surprise at his findings and changed his opinions accordingly (T. W. Todd, 1928d, 1928e, 1929b). Todd also anticipated future work when he employed a rudimentary form of modern scientific hypothesis testing in his cranial papers, using the standard suppositions of Broca and Gratiolet as null hypotheses (Todd and Lyon, 1924). Todd's findings even altered his deep-seated typological beliefs over the course of his career (A. Todd, personal communication, 8 June 1995; Jones-Kern, 1997, p. 351–378).

The conservative nature of Todd's pronouncements had two important long-term effects on the significance of his work. First, because Todd generally avoided committing his personal assumptions to print unless he felt they were proven beyond a reasonable doubt, much of his work was still of genuine scientific value by the end of the century. The same is not true for contemporaries such as Hooton, much of whose major work is now primarily of historical interest (Jones-Kern, 1997, chapters IX and X). Second, his reticent scientific conclusions led later investigators to misinterpret his personal beliefs on issues such as race. As demonstrated above, Todd was quite progressive for his field and his time on racial matters. However, because his personal beliefs were not sufficiently scientifically proven, he avoided the written expression of his racial theories in his scholarly works. This successful masking of his egalitarian "bias" led later investigators to the natural assumption that Todd was a "mainliner" and

a "moderate" regarding race (Barkan, 1992, p. 95–108), and is a testament to both his unbiased personal nature and his "facts first" scientific philosophy (Jones-Kern, 1997, p. 353–378).

Another extremely important and enduring component of Todd's personality affected his professional life in a more general manner: an abiding loyalty to Great Britain, his native country. Unlike Ales Hrdlicka (a Czech nationalist who resented the Austro-Hungarian Empire) and Franz Boas (a political liberal who resented the Junker aristocracy and blatant anti-Semitism of the German Empire) Todd never gave up his native citizenship or became a naturalized American citizen. He was born and raised at a time when the British Empire was reaching its peak, and although of Scots ancestry, was extremely proud of his British heritage. As mentioned above, he enlisted in the Canadian Army to provide his services for the Commonwealth in World War I, and stayed current with British news by subscribing to the *Manchester Guardian Weekly*. He returned to England on several occasions both before and after World War I, in 1914, 1921, 1925, 1928, and 1931, always stopping at his Nottingham tailor for more of his trademark English gray suits (A. Todd, personal communication, 8 June 1995; M. Gaylord, personal communication, 22 July 1996). Even in death he expressed his devotion to his native land by arranging his burial in as close as he could manage to "British soil"—in Foot's Bay, Ontario, near his beloved Muskoka retreat (A. Todd, personal communication, 8 June 1995). This deeply-held native loyalty was significant professionally in making Todd immune from the American exceptionalism that marked many of his peers (Jones-Kern, 1997, chapter VIII).

Todd's deliberate choice to remain an Englishman in America also had professional liabilities of which he was well aware. Franz Boas in the early 1930s endeavored to get his colleague accepted into the citizens-only American Academy of Science. Boas wired Todd to ask if he had considered becoming naturalized (Boas, 1930). Todd immediately replied with a telegram stating, "Circumstances prevent my becoming an American Citizen except in spirit" (T. W. Todd, 1930c). By way of explanation, Todd a few days later sent an uncharacteristically personal letter to Boas, one immigrant to another, which came as close to betraying a feeling of self-pity as anything he ever wrote:

I appreciate very greatly your asking me this question and I do not hesitate to speak with you of these deeper feelings though I do not usually refer to them before others. I have studied the alien problem in this country very carefully and very sympathetically and I do not believe that it is possible to eradicate loyalties [*sic*] which are mordanated into one's very being. Our children born on this soil can be and are American in feeling as well as in being but I myself, in fulfillment of the principle, must forego all privileges which might accrue [*sic*] as a result of changing my nationality. I should feel that I had obtained these privileges on false pretenses. I readily admit that I would be more comfortable if I could see things in another way for my own country has long forgotten me and treats me with the studied neglect which has been her extravagant gesture to all those who have wandered beyond her frontiers. Loyalties [*sic*] however are deeper than happiness or satisfaction. I have worked and shall continue to work with all energy and thoroughness of which I am capable for the solution of problems which beset the United States of America but I beg to keep this one little corner of my heart intact for a personal loyalty to what is fast becoming no more than a memory. (Todd, 1930d)

References to his own country forgetting him and treating him with "studied neglect" alluded to membership in the Royal Society, the most prestigious scientific body in England, the American equivalent of which is the Academy of Sciences. At that time the Royal Society rarely inducted members who lived overseas, and Todd had grudgingly resigned himself to this fact. One of the bitterest ironies of Todd's life, then, is that even as he was dying in Cleveland in 1938, Sir Arthur Keith was well into the process of pushing an initiative of Sir Sidney Harmer and other British anatomists to get his old friend elected at last (Keith, 1939a, p. 353).

The lack of recognition from the country to which he remained so steadfastly true wounded Todd deeply, and may in part explain some of his career choices. Because Todd was so hard-working and ambitious, he rarely turned down an opportunity to increase his standing in the field. Although he was not particularly class-conscious, his letter to Boas reveals a certain professional status-consciousness. Seemingly barred from the highest accolades awarded to both British and American scientists, Todd rarely refused membership to any exclusive professional group or committee, even when overburdened with other duties and responsibilities. Perhaps he would have taken part in these organizations anyway—Todd was what is now known as a "joiner." By the time of his death he had belonged to more than 60 professional and civic organizations, and he is not known ever to have officially quit his membership in any of them (T. W. Todd, 1912, 1938f). Knowledge of this is very important not only in understanding his seemingly incongruous membership in the Galton Society, but also the significance of his failure (indeed, his explicit refusal of an invitation) ten years later to join with many of his professional peers in the American Eugenics Society (T. W. Todd, 1931c; Jones-Kern, 1997, chapters VIII and XI).

All of the above-mentioned traits were integral parts of Todd's persona, but they do not aid in the explanation of how he occasionally inspired controversy and hard feelings among his peers. Todd was strong-willed, sometimes to the point of driving his colleagues to extreme irritation. This especially distressed Ales Hrdlicka (who knew Todd well and held distinctly mixed feelings about him) on more than one occasion (see for example, Hrdlicka, 1938). When Todd opposed the formation of Hrdlicka's long-planned AAPA, Hrdlicka nevertheless asked that an invitation be extended to him, remarking that, "[he] could be very obstinate if rubbed the wrong way. Yet we want him for he is one of our most deserving and hard workers" (Hrdlicka, 1930a). Todd's strong will was a crucial component of his personality, and profoundly influenced perception of him by both peers and later investigators. In particular, it played a large role in his professional and administrative style, a revealing example of which was his troubled chairmanship of the Committee on Child Development.

The Committee on Child Development: A Case Study of Todd's Professional and Administrative Style

Among Todd's numerous appointments and professional services was a stint with the National Research Council's (NRC) Committee on Child Development (CCD). Alice Boardman Smuts (1985) has documented Todd's turbulent tenure with the CCD in a revealing article from which most of the next two pages are drawn. Founded in 1916, the NRC coordinated the activities of the American scientific community to the nation's defense needs (Smuts, 1985, p. 108–109). After World War I ended, the Council continued with the mission of devoting its

resources to the needs of American society. A key component of the NRC was its use of the social and behavioral sciences, not just to alleviate, but to actually prevent, social ills. Starting with a sociology section, in 1919 the NRC added a Division of Psychology and Anthropology. When the NRC created the CCD five years later to coordinate and support child development research, it put the CCD under the control of this division. Unlike other social remediation organizations, the CCD's goal was strictly scientific in nature, and throughout its history it scrupulously avoided involvement in such edifying measures as child welfare or parent education. The CCD's purpose was strictly to promote the scientific foundation underlying all such measures, while remaining untainted itself by popularization.

In October 1927, the CCD decided to expand its membership to reflect a more interdisciplinary orientation (Smuts, 1985, p. 111–112). Comprised at that time of a psychologist and the heads of child development institutes, the committee added a pediatrician, a biochemist, a nutritionist, and an anatomist (Todd) to its ranks. Todd's election was a logical one for the CCD, as he was the only prominent anatomist conducting significant research in the problem of child development. For the next five years, he served on the committee, and when the CCD's chairman resigned his post (but not his membership) for health reasons, the committee appointed Todd to fill the vacancy.

Todd was a natural choice to be the new chairman. Apart from his seemingly boundless energy, his reputation in the field of child development had grown immensely during his five years on the CCD (Smuts, 1985, p. 112–116). He was already an associate editor of the *Journal of Child Development* and his work with the Brush Foundation was gaining nationwide attention. In addition, he had participated in the 1929 to 1931 White House Conference on Child Health and Development (WHC), as well as the WHC's Follow-up Committee, a rival group that appeared to duplicate the CCD's purpose. Because of this, the Rockefeller Foundation, which had been funding the CCD directly, decided that all of the committee's future appeals for funds would have to be submitted to and approved by the Psychology and Anthropology Division and then the NRC before the Foundation would grant them. By elevating Todd, the CCD not only co-opted a member of a rival organization, but also promoted a person who had proven his fundraising capabilities even during the Depression with his Brush Foundation work. The committee members soon discovered to their chagrin that they had been all too successful.

Todd launched himself into his new duties with his characteristic vigor. Before his appointment was even official, he fired several reports off to the Division of Psychology and Anthropology proposing major changes (Smuts, 1985, p. 116–118). Among his suggestions were general organizational modifications, the conversion of the CCD's publication *Child Development Abstracts and Bibliography* from an interdisciplinary research aid to a review journal, and the founding of a new journal to popularize child development research—inaccurately asserting that the committee engaged in parent education. Perhaps more disturbing to other CCD members than Todd's attempt to shift the committee into a direction they had deliberately avoided in the past was the fact that he had done these things without the committee's approval. They became even more upset soon afterward when Todd attempted to cancel a conference (one designed to draw more sociologists into the CCD) that the committee had approved just months earlier.

Alarmed, the rest of the committee wrote to Divisional Chair Robert Lowie with their concerns, and Lowie in turn sent

a response to Todd explaining the CCD's pure science orientation and policy against popularization (Smuts, 1985, p. 117). This only encouraged Todd to try harder, repeatedly sending arguments for the new journal and drawing similar anti-popularization responses by various officers of the NRC. After attempting to get past his detractors' concerns by semantic changes to his proposals, Todd finally went over everyone's head to William H. Howell, chairman of the NRC. In Howell, Todd found a sympathetic ear to his proposals and received what he felt was a green light to "throw all my energy into future construction, unhampered by the necessity of upholding the past" (Smuts, 1985, p. 117). Feeling himself fully in charge, he set about initiating his new plans for the organization.

What Todd proposed was nothing less than the abolition of the committee's entire past program (Smuts, 1985, p. 117–118). This included ending publication of the committee's journal ("a haphazard collection ... without plan and set together without order... it is redundant for the conscientious and the informed"), closing the Washington, D. C. office of the CCD and moving all of its functions to Cleveland, and ending committee sponsorship of conferences ("a cumbersome and tedious method of bringing together diverse disciplines"). Instead (and contrary to the founding principles of the organization), Todd proposed the CCD use the rest of its budget to take up basic research *itself* on "somatic development, mental growth and emotional expression in their interrelationship," with initial research focusing on his own field of physical development. In addition, the CCD would have the right to apply through the NRC to get financial support for local programs the committee could integrate into its own research (perhaps Todd's recently financially-pinched Bolton and Brush Surveys?).

A. T. Poffenberger, a Columbia psychologist who had replaced Lowie as divisional chair, initially supported Todd's plans, but withdrew his blessings after briefings with other committee members (Smuts, 1985, p. 118–119). Still thinking he had approval from Howell, Todd forged ahead anyway. Already incensed at their chairman's tactics, the committee grew outraged at his next move. Todd sent a letter to all CCD members on 24 August 1932 stating that their memberships had terminated on 30 June but were "renewable at the chairman's discretion" (Smuts, 1985, p. 119). Describing his program now as an NRC "mandate," Todd stated that they should notify him if they were willing to accept its conditions. On the other hand, if they found the mandate's conditions to be unacceptable, he ominously warned them to "consider carefully, in the interests of child development, your responsibility in remaining on the committee" (Smuts, 1985, p. 119). In other words, if any member now opposed him, Todd would throw him off the committee.

This flagrant excess of Todd's authority brought divisional executives into the fray, and they tried to get Todd to arrange a meeting of the CCD and the division (Smuts, 1985, p. 119–120). Todd stated that he would be happy to come, but would not invite other CCD members for financial and procedural reasons. From August to November, Todd met repeated requests for a meeting with cordial refusals accompanied by his optimistic assertions that the committee would soon come around to his way of thinking, and stating that NRC endorsement was a prerequisite to any official action. Apparently Todd was waiting for Howell to return from a long overseas trip to support his proposal as NRC chair. If this was his hope, it was a mistaken one. Howell sent a letter to Todd in mid-October stating that all plans first had to receive CCD approval. Todd gratefully replied as if the committee's

autonomy were exactly what he had desired all along. The committee finally met in November, scrapping Todd's plans and adopting a proposal along its original functions.

Despite this setback, Todd did not completely surrender (Smuts, 1985, p. 120–121). He submitted a copy of the minutes of the meeting to the division without the approval of the committee. Among other things, they stated that the committee had agreed to take on a full-time field secretary hired by the chairman and to convert the *Abstracts* immediately into a review journal. Although two CCD members later approved the minutes, two other members strenuously objected to them. When the committee's report came before the Divisional Executive Committee (DEC), they accepted most of the program, but refused the request for a field secretary and stated that the *Abstracts* would at least finish out the current volume in its present configuration out of deference to its subscribers. Afterward, the DEC stated that the committee could gradually convert *Abstracts* into a résumé service, but not a review journal.

Now it was Todd's turn to be incensed (Smuts, 1985, p. 121–122). Defending his tenure as chairman and insisting that he had received "authoritative advice" (Smuts, 1985, p. 121) in October to support his present actions, Todd sought to terminate not just the journal but also the CCD itself. He told the DEC that its actions regarding *Abstracts* were too late, that he had already disbanded the journal's subcommittee, laid off its Washington stenographer, and canceled all subscriptions. Furthermore, based on the same vague "authoritative advice," he stated that he was now prepared to fulfill his duties as chairman by providing for "an effective termination" and "decent interment" of the CCD (Smuts, 1985, p. 121). Poffenberger discussed Todd's fiat with other committee members, and then responded by reversing all of Todd's recent actions and reminding him that only the NRC could disband the CCD. In addition, because Todd had stated that he could not continue as chair without the reimbursement for services and expenses he felt the CCD owed him, Poffenberger suggested that Todd might wish to step down.

Todd's response to Poffenberger was that urgent local affairs demanded his immediate attention, but would reply at his earliest possible convenience (Smuts, 1985, p. 122–124). Eleven days later, still having received no response, Poffenberger wrote to the committee members asking if they should dissolve and immediately reconstitute themselves minus Todd. Todd had actually sent a letter on the same day asking Poffenberger for a meeting, but the Division head had already made up his mind. By unanimous consent of the committee and the blessings of the DEC, the NRC's Executive Board first disbanded the CCD and then reappointed everyone but Todd to the new committee. Notified by letter in mid-February, Todd responded with an earlier-prepared report recommending the dissolution of the CCD and a letter stating, "I am sure that your feeling of relief must equal my own that the final stages of this discussion have been passed through with such ease" (Smuts, 1985, p. 124). The incident had damaged the credibility of the CCD in the eyes of many in the Rockefeller Foundation and the NRC, and these groups withdrew some of their previous financial support. Nevertheless, the organization survived and launched the still-extant Society for Research in Child Development.

Todd's turbulent tenure as CCD chairman was not his finest hour. However, it was an instructive episode in his idiosyncratic professional and administrative persona. In particular, this incident illustrates Todd's executive philosophy, his style of professional correspondence, and what he felt his primary

professional role was. Knowing about these characteristics is extremely important in making sense of other aspects of Todd's career and correcting misconceptions derived from previous examinations of his writings.

For example, Todd's actions as CCD chair seem strange in the light of his interdisciplinary disposition. The CCD at its very heart was a group designed to promote interdisciplinary research, yet Todd tried to alter its function significantly. One can only begin to understand such behavior by taking into account Todd's ideas of his professional role. Throughout the course of Todd's career (and especially after he assumed the directorship of the Brush Foundation), he increasingly became convinced that the aspects of physical anthropology dealing with growth and development deserved wider popularity and use to serve edifying, practical social ends. This is ironic for two reasons. On a larger scale, the trend in most of the social sciences at this time was in the opposite direction toward pure research free from the taint of advocacy or populism (Furner, 1975). Also, in the narrower field of physical anthropology, Todd vehemently opposed the practical application of his field in its traditional investigative focus: race research (Jones-Kern, 1997, p. 349–378). Although Todd's philosophy was fundamentally different from the professed purpose of the CCD, he saw his chairmanship of the body as an opportunity to expand the edifying work he executed in Cleveland. Despite repeated attempts by committee members to explain the principles underlying their opposition to him, Todd relentlessly insisted on pursuing a popular and practical course, even going so far as to refer Division head Lowie to a popular article in *Science News Letter* as a model for the kind of journal into which he wanted to turn *Child Development Abstracts* (Smuts, 1985, p. 117). Todd's increasingly intense commitment to his personal brand of applied, practical, interdisciplinary research overrode his dedication to the theoretical, "pure" academic integration fostered by the CCD, which he felt accomplished little with its available resources. Because these two philosophies were fundamentally at odds, one can more easily understand the showdown forced by Todd, his attempts to kill the organization, and his eventual ouster. Yet a knowledge of Todd's practical scientific inclinations alone is insufficient to understand Todd's actions as CCD head.

Another key component of Todd's personality was his conception of executive authority. Todd was a firm believer in administrative and professional hierarchies. As such, he served obediently and deferentially in subordinate roles, but expected full executive power when placed in positions of leadership. There are many examples of this general hierarchical philosophy from his life and career. It would be tempting to suggest that this was a product of his military career (and indeed his World War I captaincy may have reinforced his commitment to the chain of command idea), but Waite's (1946, p. 389, 408) disapproving description of Todd's departmental reorganization in 1912 indicates that these proclivities were already apparent when he reached American shores. As discussed above, Todd's anatomy lab was a well-defined hierarchy with himself as the supreme executive, and Todd assumed administrative powers bitterly contested by other professors (Waite, 1946, p. 389, 408; Western Reserve Medical School, 1917a, 1917b). Some similarly viewed his Brush Foundation chairmanship as autocratic—although other members of the Board felt free to express their opinions on the organization's role, there was little question that the Foundation was subservient to its chairman's wishes. This stands in stark contrast to the cooperative and deferential nature Todd displayed when not in a position of authority. Despite his actions as chair of

the CCD, Todd had served the committee sufficiently well and smoothly enough beforehand that it not only chose him to lead the group in 1932, but was also shocked by his subsequent behavior. Like any good soldier, he obeyed his superiors, but expected to be obeyed by subordinates. A sudden change in roles brought a corresponding sudden change in attitudes. For example, even during his short tenure as president of the AAPA, there was a marked change in the tone of his correspondence before and after his appointment. His ordinary cordial reserve immediately turned into a stiff formality, and opinions that he had respectfully tendered in preceding years soon became policy by executive action (T. W. Todd, 1938b, 1938d). One should not confuse this behavior with mean-spiritedness. Ales Hrdlicka, who had his share of differences with Todd, explained his friend's actions to a colleague by stating that he was "not vicious, only ingrown and stubborn" (Hrdlicka, 1938). While his executive manner also included liberal doses of delegation and diplomacy, there was never any doubt whose word Todd felt was final.

As indicated above, the tone of Todd's correspondence was another important and occasionally misunderstood aspect of Todd's personality. His writing was in many ways an extension of the cordial style that enabled him to maintain warm personal and professional relationships with people of radically different beliefs and opinions. In both correspondence and print, Todd habitually tempered his criticism with compliments, joviality, and acknowledgments of common ground. This was a practice he not only scrupulously followed himself, but expected his students to follow as well. Cobb (e.g., 1959, p. 236-237; 1981, p. 519-520) made frequent note of his mentor's cordiality and avoidance of answering criticism with criticism. Krogman, too, acknowledged Todd's pervasive civility, both in print and in personal correspondence. For example, in a 1934 letter to Cobb, Krogman described a paper he had recently given in Boston that was critical of several other investigators. In noting the graciousness of the way the paper phrased these criticisms, Krogman (1934) remarked, "You will of course recognize the Chief's deft touch here and there, especially when I found myself unable to say a single thing good about either MacDonald's, Watkins's and Evan's papers." Only when he was at his angriest—usually when an editor attempted to edit his works without his approval—was Todd prone to send a response of unmitigated contempt. Even in these instances, however, Todd always avoided profanity and direct insult (T. W. Todd, 1936b, 1936c; Jones-Kern, 1997, appendix B).

A case in point of Todd's correspondence style was his attempt to get his book review of H. S. Jennings' *The Universe and Life* published. Robert Lowie originally solicited the piece for the *American Anthropologist*, but was replaced as editor by Leslie Spier by the time Todd sent in the review (Lowie, 1933, 1934; T. W. Todd, 1934b). Spier rejected the piece on the grounds that the book was insufficiently anthropological in scope (Spier, 1934a; T. W. Todd, 1934c). Never one to give up easily, Todd wrote back that the situation embarrassed him and wondered aloud about its justification and ethicality. The book, he explained, applied to humanity in a general manner and the journal had already accepted it from the publisher for review. Stating that he had "no personal feelings in the matter," and offering to pare the item down, Todd resubmitted his manuscript (T. W. Todd, 1934d, 1934e). In a tactful response, Spier again refused to print the review, and reassured that the publisher's gift of a book implied no obligation on the part of a journal to review it (Spier, 1934b). Todd ended the correspondence with Spier in his characteristi-

cally amiable manner: "Many thanks for your letter of March 23rd which completely clears my conscience! The review is of no material significance. It was only our possible obligations which gave me some concern" (T. W. Todd, 1934f). The complete ingenuousness of this statement is questionable. Todd immediately sent his review unsolicited to at least one other journal before *Science* finally accepted it (Cattell, 1934). Although this was a relatively minor incident, it is an excellent demonstration of the manner in which Todd could sometimes politely profess agreement and accord even when his personal sentiments differed profoundly.

As may be surmised, Todd's unique style of correspondence occasionally confused his peers. Sometimes, his cordiality and emphasis on common ground resulted in a misinterpretation of his true sentiments. This is particularly evident in the correspondence surrounding Hrdlicka's abortive attempt to form the AAPA in 1924 and Hooton's and Boas's attempt to craft a professional statement on race in 1935 and 1936. At other times, his efforts to diffuse rancor and criticism by the use of compliment and vague prose left his correspondents completely baffled. In the heat of the CCD controversy, Todd sent a letter to an antagonistic committee member stating that the non-proactive function of the committee—a function which Todd openly opposed—"not only still holds good ... but is the clearest and most compelling definition of our purpose" (T. W. Todd, 1924c). This statement, along with three additional pages of explanation led the Division head to query the letter's recipient, "Did that confuse you still further?" (Smuts, 1985, p. 120). Todd's correspondence in response to the international committee to standardize anthropometry inspired similar bewildered appraisals (although part of this confusion also stemmed from the inability of his peers to understand Todd's basic premise) (e.g., Pearl, 1936; Hooton, 1936).

The misinterpretation of and confusion over Todd's correspondence was not solely a problem of his contemporaries, however. Later researchers who have read some of Todd's correspondence may have confused his responses crafted to minimize contention as tacit agreements with the positions to which he was replying. Todd's cordial responses to frankly racist letters by Charles Davenport, for example, seem to have led at least one investigator quite understandably to believe that Todd was a "mainliner" regarding race (Barkan, 1992, p. 73). A closer reading of this correspondence with a knowledge of Todd's style and personal opinions yields a much different interpretation, especially when compared to the concurrent correspondence he conducted with the racial egalitarian Boas. Todd confined his racial discussions with Davenport to purely technical and descriptive issues, let blatantly racist statements pass without comment, and accepted reprints of Davenport's racist papers with politely vague but noncommittal thanks such as, "[I] am interested in skin color" (Todd, 1925a), "I am very glad to have this for my files" (1928f), and "it is interesting to get these data together" (1925b). In contrast, Todd's letters to Boas display an unequivocally active sympathy and agreement with his racial and environmentalist views (e.g., T. W. Todd, 1923b, 1928g, 1930d, 1933c, 1934a).

Todd occasionally created outright confusion in his writing as well. In her account of Todd's tenure as CCD chair, Smuts (1985, p. 117) states Todd's written recalcitrance was "pleasantly" and "cheerfully" firm, adding that "[a]vowing agreement with the opposition while persisting in arguing for his own program was a tactic Todd used repeatedly." According to Smuts, Todd's

correspondence during the worst of the conflict "is like being in never-never land" (Smuts, 1985, p. 120). Such confusion is also evident in a few of Todd's printed works. In his characteristic effort to minimize disharmony and temper criticism in his review of the works of others, Todd occasionally words his critiques so abstrusely that his precise opinion is unintelligible even to a reader well-versed in his beliefs and style (myself included). A familiarity with Todd's characteristically nebulous cordiality in public criticism is thus extremely important, both for the purpose of discerning his true beliefs on certain subjects and for use in contrast to the more pointed and decidedly less amiable criticism he reserved for those with whom he vehemently disagreed (T. W. Todd, 1935a; Jones-Kern, 1997, chapter XI).

Although all of the above-mentioned personality traits provide fascinating insights into Todd as a man, they are also crucial in explaining his behavior at different times and beliefs on different issues. Indeed, most of these traits (work habits, egalitarianism, charm and cordiality, interdisciplinarianism, writing, and executive style) played a large role in his actions regarding physical anthropology's professionalization, as well as his contributions to the field's evolving positions on theory, race, and eugenics. They also provide an important key to understanding the final, often turbulent, decade of his life.

"For the betterment of mankind": Todd's Final Years, 1928-1938

The year 1928 was in many ways a watershed in the life of T. Wingate Todd. Until this point, Todd had been a well-respected anatomist and physical anthropologist who was a primarily academic researcher of extremely diverse scholarly interests. Afterward, he became an increasingly public personality who oriented his research toward more and more practical ends and focused mostly on the issue of growth and development. The following decade brought Todd to the pinnacle of his profession, witnessed the greatest bulk of his publications, introduced him to most of his important students, and saw him take an ever greater popular and public role. It also brought increasing health difficulties and eventually an untimely death. The catalyst in Todd's efflorescence was a series of tragedies that befell one of Cleveland's leading citizens, Charles Brush.

The Bolton-Brush inquiries

Charles Francis Brush by 1928 had gained the reputation of being one of America's great inventors. A University of Michigan graduate in mining engineering, he made his greatest contributions in the field of electricity. In 1876 Brush made the age of electricity possible by inventing the open-coil dynamo, the world's first practical producer of high-tension current. The following year he created the first practical electric arc light, which nurtured into being not only the electric-power but also the carbon-electrode industries. Brush's many other important electrical inventions of subsequent years included the compound-field dynamo (predecessor to the constant-potential generator), the process for producing electrolytic aluminum, and the first practical storage battery. His successful electric company eventually became a part of General Electric. In addition, the inventor made numerous contributions in fields other than electricity, including the invention of the first practical process for making liquid air and the discovery of helium in the earth's atmosphere in 1895 (Hall, 1946, p. 3-5). By the time of his death in 1929, Brush had acquired several honorary doctorates, the

Rumford Medal of the American Academy of Arts and Sciences, the Franklin Medal of the Franklin Institute, the Edison Medal of the American Institute of Electrical Engineers, and France's Legion of Honor, and had lit the streets of America, Europe, and Asia (Hall, 1946, p. 3-5; Brush Foundation, 1958, p. 3-4).

However, all of Charles Brush's inventiveness, wealth, and prestige could not prevent the tragedies that afflicted his family. His wife died in 1902, and afterward doctors discovered that his youngest daughter had an incurable mental illness (Wood, 1983, p. 60). Although Brush denied it at first, even to the point of staging a "ghostly" debut for her, he came to accept the fact of his daughter's schizophrenia and grew increasingly despondent. Then, in 1927, his family suffered a series of devastating blows. In March, an automobile struck and killed his oldest daughter's thirteen-year-old son. Two months later, his son Charles' daughter Jane fell gravely ill. Charles Jr. was living in Cleveland at the time, employed conducting crystal research in his father's Cleveland lab. When his daughter entered Mount Sinai Hospital, the doctors said her only hope was a blood transfusion. He readily agreed to be his six-year-old's donor, and as was the practice at the time, doctors inserted a rubber hose with needles on either end into Charles Jr.'s and Jane's arms. Not only was the transfusion unsuccessful, it resulted in a case of septicemia (blood poisoning) that killed them both.

Because the 34-year-old Charles Jr., a physician, had gotten his father interested in the issues of population control and eugenics before his untimely death, the elder Brush decided to memorialize his namesake in the form of a Foundation to further these goals (Wood, 1983, p. 60). In 1928 Charles Brush Sr. donated \$500,000 of his stocks and bonds to create the Brush Foundation (Bailey, 1992, p. 29), an organization he wanted to serve "for the benefit of mankind" (Brush, 1928). The preamble attached to the deed of gift (later negligibly altered for publication) revealed much about the senior Brush's philosophy and goals for his organization (Jones-Kern, 1997, appendix C). The main emphasis throughout the document was on population control, although the vague references to "betterment of the human stock," "the weak and unfit," and "research in the field of eugenics" indicated a secondary focus on more traditional eugenic themes (Brush, 1928).

Brush was the organization's sole benefactor, but had no interest in being its head and courted his family and friends for suggestions on the Foundation's directorship (Wood, 1983, p. 60). His son-in-law, Roger Perkins, had been instrumental in lobbying the Ohio General Assembly to allow Todd to build his osteological collection (see above) and urged Todd's appointment (Wood, 1983, p. 60; Bailey, 1992, p. 29). As a hard-working, persuasive, well-rounded skeletal anatomist with a particular interest in children, Todd was a natural choice for the job. Todd readily accepted, and turned the foundation's major research thrust toward the immensely significant complex of projects later known as the Bolton-Brush studies (Hall, 1946, p. 4-20; Brush Foundation, 1981, p. 5-24).

Soon after accepting the Brush Foundation directorship, Todd convinced its Board of Directors to make their first major project an analysis of normal child growth and development. This was a natural outgrowth of both his lifelong interest in children's health and his major research emphasis on growth and development. As discussed above, Todd held a deep and personal interest in the health of the young going back to his own early illnesses and his original professional plan to go into pediatrics (Cobb, 1959, p. 233-236). The lures of Egyptology and anthropology shifted him from this course, but issues of growth and

development remained a subtext of his early professional life. Starting in the 1910s with his cervical rib studies, Todd by the early 1920s had published the most important papers to that time on age-related changes in the adult skeleton and had become one of the world's experts on the subject. As he completed this cycle of papers, Todd began to turn his attention to similar issues in pre-adults. However, when Todd began to merge his interests in children and growth in the mid-1920s, he ran into a basic problem: How exactly could such a study be done with the resources available? Todd faced seemingly intractable material and methodological difficulties (Keith, 1939, p. 350).

To this point, materials had been the least of Todd's problems. He had conducted all of his major age-change research on the rapidly-increasing osteological collection at his disposal. The unique nature of this assemblage allowed Todd to select a group of individuals of known age to correlate with observed skeletal changes. Todd deliberately excluded individuals known to have suffered from long-wasting illnesses from his analyses so his sample would approximate that of the "normal" population. However, this approach was impossible for a study of children for two main reasons. First, there were relatively few children in his collection (T. W. Todd, 1929c, p. 5-6). The cause of this was largely demographic. After infancy, children suffer a lower mortality rate than the rest of the population (Coale and Demeny, 1983). Furthermore, those that did die at this time were less likely than adults to remain unclaimed by their parents. Only those few children from the most destitute of social conditions were available to Todd for curation into his collection. Second, and related to the first, most of the children Todd had included in his assemblage had visibly suffered from the medical and nutritional privations of the lowest socio-economic strata. Because normal childhood growth is deeply dependent on adequate food and freedom from prolonged illness, the majority of the children unfortunate enough to be part of the Hamann(-Todd) osteological collection were simply unfit for Todd to use as yardsticks for a study of normal childhood growth (T. W. Todd, 1929c, p. 5-6 and 1929d, p. 6-7). The quantity and quality of the skeletons available for his use forced Todd to abandon the method he had used for his adult development studies and look elsewhere for research materials (Hall, 1946, p. 4-6).

Compounding these material shortcomings were some major methodological difficulties. When Todd took up the problem in the mid-1920s, there was neither a clear understanding of what constituted normal childhood growth, nor a consensus on how to study it. Indeed, most of the physical-anthropological community looked down upon the whole idea of growth studies as being unworthy of examination: Earnest Hooton once stated that growth research "merely shows that older children are bigger" (Garn, 1981, p. 521). Perhaps because of this professional antipathy, by the early 1920s only a few large studies concerning this question existed. These had been largely outside the field of physical anthropology and suffered from a severe methodological handicap. Most research until this time had focused on trying to discern general principles from the comparison of average measurements. For example, investigators took a measurement such as "stature" from a number of children of the same age, and assumed the mean value derived therefrom was the norm for that cohort. However, the wide range of normal variation in size found among children from different family lines and development patterns greatly frustrated this approach. By these standards, a relatively small child born of relatively small parents, even if his or her nutrition and health had always been optimal, was

"underdeveloped," as was the child whose genetic make-up was that of a "late bloomer" (Garn, 1981, p. 523-529). Todd saw the problems inherent in the prevailing method, and set out to conduct his own investigation of the problem in hopes of finding a better way. In the process, he helped revolutionize both the theory and practice of growth research.

One of the major innovations Todd brought to growth research was a new conception of growth itself. Rather than being a simple issue of "getting bigger" or a series of static biological moments, Todd felt growth was a dynamic, unfolding process with both quantitative and qualitative aspects (Krogman, 1939a, p. 163-175). Accordingly, Todd redefined growth into three closely related phenomena: people "grew" (increased in dimension), they "grew up" (changed in proportions and adjusted body parts), and they "matured" (biological time passed in the tissues) (Krogman, 1951, p. 679-687). Only when researchers examined all three of these dynamics together, he believed, was a real understanding of growth possible. Previous studies had generally focused only on the first part of this complex (above or below a certain mean for a certain age), and thus shed no light on whether the rate or trajectory of growth in a given individual was satisfactory (Tanner, 1981, p. 321). The shift in emphasis inherent in this approach from an obsession with size to a developmental process required a new gauge by which one could measure the phenomenon (T. W. Todd, 1932a, 1937a). Todd developed one, but not without resistance from within the field.

Over the course of his growth investigations, Todd increasingly began to take the controversial opinion that mean size measurements were of minor importance in assessing normal growth. Such crude measures did little to account for the many social and hereditary factors that influenced development. He had no theoretical use for the "fat" but "water-logged" babies held up as a model of health, nor did he accept that researchers should take as standard growth studies conducted using children who had suffered privation (Frank, 1962, p. 12-15). Instead, he insisted that scientists could only find a true standard of normal growth by first discovering a method that did not rely on gross measurement and then conducting an examination of children for whom adverse social or nutritional circumstances had not affected development. The former concern led to the "family line" concept and the "bone age" method, and the latter led to the idiosyncratic criterion of selection of participants to the Brush Inquiry (Krogman, 1939a, p. 169-175).

Both the "family line" and "bone age" ideas were almost entirely new to growth research. Todd meant the "family line" idea to address the previously-mentioned problem of the well-developed child of unusual size. Todd insisted that there were a great many people of perfect health whose large or small size was mostly a result of their hereditary endowments (T. W. Todd, 1932a, p. 258-279). Normal growth, then, was a relative term applying to family lines of small, medium, and tall growers (Krogman, 1951, p. 684). While Todd (1935b, p. 181) freely admitted that heredity was "a broad stream" affected by many other factors, his "family line" concept shook the conventional wisdom of growth research and made a reliance solely on mean anthropometric measurements obsolete as a technique in determining normal development (Krogman, 1939a, p. 170-175).

An acceptance of the "family line" idea caused a critical problem, however. If mean measurements alone could not determine normal growth, what could one use in their place? To surmount this obstacle, Todd pioneered the technique of "bone age" (Frank, 1962, p. 12-15). The human skeleton is originally

cartilaginous, and gradually ossifies (turns to bone) from the embryonic stage until adulthood. However, the rate at which bones ossify varies significantly. Some bones are mostly ossified at birth, others do not complete the process until decades later. The latter is particularly true of the clavicle (collar bone) and many of the bones of the extremities. These maintain cartilaginous growth plates at either end that allow the bone to lengthen for many years until the diaphysis (middle part) finally fuses with the epiphyses (ossified ends) (White, 1991, p. 20–23). Greatly refining an idea first proposed by T. M. Rotch about fifteen years earlier (Rotch, 1908, 1909), Todd realized that if he could find a standard pattern of epiphyseal fusion to correlate with chronological age in a series of unquestionably healthy and well-nourished children, he would have an accurate “yardstick” of normal growth free from the problems inherent in taking raw measurements (Frank, 1962, p. 12–15). All he needed to accomplish this was an x-ray machine and a group of healthy children. The Brush Foundation and the selection methods of its Health Inquiry provided Todd with these materials (Tanner, 1981, p. 320–323).

Todd had actually begun his studies of normal childhood growth two years earlier. Using a modest grant from the Cleveland Health Council, Todd conducted a study on the health of 600 well-developed students in the Stearns Road Grade School. Encouraged by the results, in 1927 he decided to begin a more in-depth and longer-term examination of children's health. With the support of the Cleveland Board of Education and the staffs of two public schools, Todd set up a summer health “contest” for youths between six and fourteen years of age. In reality this was the beginning of a proposed three-year exploratory health study. He and his assistants took anthropometric measurements, assessments of current health, radiographs of six areas of the body, behavioral response tests, and family backgrounds of the children involved. They referred children with health problems to family physicians, and gave the “winners” a trip to summer camp sponsored by the Cleveland Welfare Federation and the local press (Behrents, 1984, p. 10).

The project continued and expanded in the summer of 1928, with some of the original group and a number of new students examined. The recall of previously-studied children officially made the undertaking a longitudinal study; one in which researchers investigate the same people year after year to discover general patterns and changes. Because longitudinal studies are difficult to organize and necessarily run over prolonged periods, large ones are rare and expensive; and the Stearns Road examinations ended abruptly the same year due to funding problems (Behrents, 1984, p. 10–13). However, Todd's summer program had begun to receive national recognition and financial support. In October, the longitudinal “Health Inquiry” was the first research program undertaken by the newly-formed Brush Foundation and received financial aid from the Laura Spelman Rockefeller Fund (Hall, 1946, p. 5). Soon thereafter, other philanthropic institutions added matching funds, including the General Education Board of the Rockefeller Foundation and the U.S. Public Health Service. However, the study's most important beneficiaries remained the Brush Foundation and another philanthropy formed in the same month: the Charles Bingham Bolton Fund (Behrents, 1984, p. 10–13).

Like the Brush Foundation, the Bolton Fund was the product of a family tragedy. Charles Bolton, son of local philanthropist and future congresswoman Frances Payne Bolton, had become a paraplegic in a swimming accident at the age of nineteen (Bailey, 1992, p. 29). His orthodontist was Todd's former graduate

assistant and fellow craniostat inventor B. Holly Broadbent. Todd and Broadbent encouraged Mrs. Bolton to fund an allied project to the Health Inquiry that would focus on normal dento-facial growth. Officially independent of Todd's Brush examinations, the Bolton study worked in close conjunction with Todd's, sharing many of the same children as participants. Todd also served on the Bolton Fund's Board of Directors (Behrents, 1984, p. 4–16).

In late May of 1929, the Brush Foundation officially formed the Brush Inquiry, a Cleveland center for the longitudinal study of children. Two weeks later, Brush died at the age of 80, and willed a five-year grant-in-aid to extend Todd's project into a “comprehensive longitudinal study of the attributes of healthy growth” (Behrents, 1984, p. 10). In 1932, in order to keep all studies and finances coordinated, the various organizations formed the Developmental Health Inquiry of the Associated Foundations and named Todd its director. This entity drew support from the Brush, Bolton, Spelman Memorial, and other funds. The following year, the Edna Perkins Fund for the study of Adolescent Tuberculosis, recently founded by Charles Brush's daughter, named Todd as its Director of Research. This became yet another resource for the Brush Inquiry. In conjunction with the other finances available, it allowed the Brush Inquiry to continue even during the worst of the Great Depression (Behrents, 1984, p. 10–23). Despite these valuable backing institutions, however, the Brush Foundation deeply felt the economic crisis that afflicted the world at that time. Because Brush endowed the organization with stocks and a few bonds, the stock market crash drastically reduced available funds. In early 1931, the Medusa Cement Company (which accounted for almost all of the Brush Foundation's holdings and income) halved their share dividends, and consequently also cut the Foundation's budget nearly in half (Brush Foundation Board, 1931a). Further crippling was the unexpected exhaustion of the additional funding provided for in Brush's will, originally intended to last five years (Brush Foundation Board, 1931a, 1931b). This predicament had repercussions that lasted years. A number of Brush employees had to be laid off at the end of the year, and the original Brush Publication series (discussed below) ceased soon afterward (Brush Foundation Board, 1931b, 1932). The reduction of staff slowed work and placed an even greater yoke on Todd's already overworked and ailing shoulders. In addition, the sudden financial crunch put the Foundation in an embarrassing position in relation to the University. The organization earlier had purchased a facility used to house research animals on terms negotiated before the reduction of dividends (Brush Foundation Board, 1930). Western Reserve refused Todd's overtures to refinance the debt, thus putting an even greater strain on the Foundation's monetary reserves (Brush Foundation Board, 1932 and 1936). The animal-house debt continued to be a problem for the organization for the rest of Todd's life and even after his death (Brush Foundation Board, 1934, 1936, 1938a, 1938b, 1940a, 1940b).

These economic difficulties also may have had a significant impact on another otherwise confounding event in Todd's career: his stormy tenure as the head of the National Research Council's Committee on Child Development (CCD). Todd rose to this position in the midst of the financial crisis of 1931 to 1932. At the time Todd rose to the chairmanship, the Brush Foundation Board had limited its budget for the entire year of 1932 to \$8,500, sixteen percent less than that for just the second half of 1931 (\$10,135) (Brush Foundation Board, 1931a, 1931b, 1932). Immediately

upon receiving the chairmanship—indeed, even before his position was official—Todd attempted to reorganize the Committee's finances dramatically toward his research ends. Although a definite relationship cannot be proven between the Brush Foundation's loss of funds and Todd's attempt to steer CCD finances toward his research, it is not unreasonable to assume that they were at least partially connected (Behrents, 1984, p. 6–20). The hunt for funds continued to be a troubling problem for Todd, and as late as 1938 he called it “the most harassing of all my jobs” (T. W. Todd, 1938c). His wife may have even alluded to these problems as a factor in Todd's death later that year when she insisted that “anxiety and worry, not hard work alone—took toll of his life [sic]” (E. Todd, 1939).

Although always a concern, finances thereafter were not a project-threatening difficulty. Thus, Todd and Broadbent were able to turn the Bolton-Brush Inquiries into the largest and most comprehensive longitudinal growth study to date (Hall, 1946, p. 5–12). Todd at times had more than 50 assistants working for him. Todd's son (A. Todd, personal communication, 8 June 1995) remembered the number being as high as 77 at one point. Todd and his staff examined nearly 4,500 different children from 2,600 different families before the World War II exigencies forced an end to the Brush study in 1943 (the Bolton studies continued until 1959) (Behrents, 1984, p. 16–32). The studies produced more than 22,000 physical examinations, 90,000 mental and psychological tests, and between 300,000 to 400,000 radiographs—the largest collection of its type in the world (Bailey, 1992, p. 30–31).

Foundation workers examined all children enrolled in the survey every three months in infancy, every six months from age one to five, and then every year on or near their birthdays through adolescence (Bailey, 1992, p. 30–31). The Board of Education aided in recruiting, sometimes having the students in participating schools hold health contests in which school children voted for their healthiest peers to participate (Anonymous, n.d.). Being chosen to participate was an honor, and many Cleveland-area parents sought to volunteer their children because the staff would make health recommendations and referrals if they detected a problem. Although local physicians jealous of their patients ordinarily might have staged some resistance, there was none. Todd never took the Ohio Medical Board Examinations upon arriving in the United States and was thus not a practicing doctor. This reassured Cleveland family practitioners that Todd would not “steal” their patients (Behrents, 1984, p. 16–22). Upon reaching the testing center, the children donned paper gowns and slippers and took a battery of tests, sometimes taking up to two days to complete. Along with several x-rays and 25 anthropometric measurements, children also completed psychological, behavioral, strength, and eye-hand coordination tests. Other parts of the Inquiry included footprints, family histories, and a 588-item questionnaire to be filled out annually by parents. Investigators then used the huge quantities of data to conduct growth and development research in a number of different academic areas (Behrents, 1984, p. 22–32). Although there was remarkably little concern from parents of these children at the time, the frequent x-raying of young children has since raised concern about the long-term health effects of the Brush Inquiry (Wood, 1983, p. 58–59; A. Todd, personal communication, 8 June 1995). Preliminary reviews conducted by Case Western Reserve medical—and dental—school researchers revealed only a marginally higher cancer rate in Brush participants compared with the rest of the population. However, there is no conclusive proof that

the studies caused damage or that they were completely harmless. (Wood, 1983, p. 58–59).

Positive media coverage and Todd's own increasingly astute talent for public relations greatly aided his Brush Foundation efforts. The Cleveland *Plain Dealer* and *Press* gave much positive local coverage of the Foundation's work from the time of its inception. Healthy boy and girl contests for the inquiry usually merited both a story and photos of the winners. In addition, the local papers printed and sent out on the Associated Press wire reports of Todd's lectures given under the Foundation's auspices. Scores of newspapers in nearly all of the 48 states picked up these items at one time or another, giving Todd and the Foundation national exposure. Todd's lectures and speeches on the Foundation's behalf were themselves public relations instruments, many of which served doubly in that capacity by being turned into the Brush Foundation series of publications (Anonymous, n.d.).

The Brush Foundation publication series was almost solely the work of Todd himself. The first 20 of the series were original works, pamphlets usually between 7- and 20-pages long and bound (stapled) in a sturdy brown card-stock cover. Nearly all of the first 20 were reprints of Todd's speeches, the only exceptions being *Race Betterment* (No. 4, which contained speeches given at the Ohio Race Betterment Association—“Race” in this sense meaning humanity in general), and *What We Know About Heredity and Environment* (No. 7, a speech by Benjamin C. Gruenberg for the National Conference of Social Work). The total circulation of these publications is unknown, although their effects on publicity and popularization were probably marginal compared to the local—and national—media coverage the Brush Foundation enjoyed. On an historic level, though, they were important and rare written insights into Todd's personal feelings about certain issues uninhibited by his usual printed scientific reserve. For example, *An Anthropologist's Study of Negro Life* (No. 8), an address Todd delivered before The Association for the Study of Negro Life and History, was an unabashedly racially egalitarian declaration that attributed any minor differences between Black and White cranial development solely to social and environmental factors. The Brush publications are also quite revealing about Todd's place in the eugenics movement. His personal views on health, growth and development, or “race improvement,” were the themes of most of the rest of these original publications. Backed up by Todd's research, the general tenor of these pieces was that environment played an extremely large role in these matters, and that scientists must conduct much more basic research before they could make definitive pronouncements or social policy recommendations. These sentiments put Todd among the most moderate, “reform,” fringe of his contemporary eugenicists (Jones-Kern, 1997, p. 394–407). After the first 20 of these pamphlets, original publication ceased, presumably for financial reasons. All subsequent Brush Publications were simply selected reprints of previously published works stamped with a Brush serial number. Except for one by his student Krogman (No. 44), all of these 27 publications were by Todd and dealt almost exclusively with growth and development (Jones-Kern, 1997, appendix A).

The Bolton-Brush Inquiries were the central focus of the rest of Todd's career on both a professional and scientific level. Professionally, they vaulted Todd to his highest level of acclaim yet, both popularly and among his peers. The national media attention devoted to Todd's work included a major, two full-page story with photographs printed in a number of Sunday papers across the country. Speaking invitations extended to him from

coast to coast enhanced this attention (Anonymous, n.d.). Other prominent members in the field recognized his expertise, resulting in prestigious appointments to national committees on child development (discussed below) and associate editorships of both *The Journal of Child Development* (1930) and *Growth* (1937). Scientifically, these studies inspired the vast majority of Todd's scholarly work for the rest of his life and resulted in some of his most important work (T. W. Todd, 1938f).

The final years

Although the administrative duties of the Brush Foundation and its research into growth and development occupied the plurality of Todd's time for the rest of his career, he was still active in completing his own process of growth and development into one of the most important and publicly recognized men in his field. Todd was already in the public eye due to his promotion of the Brush Foundation and its research, and the media and public organizations (both local and national) increasingly called upon his expertise. From this platform he more strongly began to advocate the use of physical anthropology toward practical, social ends. However, as always, research and teaching remained his primary concern, and this period produced some of his most significant work and students.

Largely as a result of the high profile that the Brush Inquiry enjoyed in the Cleveland media, Todd's local stature grew immensely. On a professional level, the Cleveland Dental, Neurological, and Allergy Societies made him an honorary member of their organizations. Several civic organizations also began to request Todd's services. In 1931 he became a member of both the Girls Bureau Board of Advisors and the Board of Directors of the Humane Society. Named to the Cleveland Health Council in 1929, Todd was appointed chairman of the Cuyahoga County Joint Committee on Child Health and Protection three years later. In 1933, the Edna Perkins fund tapped Todd as its director of research. He served in all of these capacities until his death (T. W. Todd, 1938f).

Todd strongly believed in civic responsibility, and even though he never became a U.S. citizen, he viewed it as his duty to serve his resident community (T. W. Todd, 1934g). Already a member of numerous local groups, by the mid-1920s opportunities to serve on the national level increasingly came his way. In 1926 the Social Science Research Council named Todd to their Committee on Interracial Relations, charged with analyzing this perplexing problem of American society. Appointments to the National Research Council Committees on Human Heredity and (as discussed above) Child Development followed, as well as the White House Conference on Child Health and Protection (Medical Section) and its Ohio Follow-up Committee (T. W. Todd, 1938f). These appointments point not only to Todd's growing national stature, but also to his increasing belief in the use of physical anthropology toward practical, social edifying ends. Along with his national committee work, evidence of his trend toward active advocacy also exists in his writings of the period.

Most of Todd's publications were scholarly in nature, but starting in the late 1920s and continuing through the 1930s he increasingly authored pieces more popular in tone. All of the early Brush Foundation publications fall into this category, but their audience was extremely limited. Of more widespread significance were his items for the mainstream press. Articles by Todd appeared in the *Survey*, *Survey Graphic*, and *Cleveland Press*. Todd also wrote book reviews dealing with socially significant

issues for *The Nation*, *Parents' Magazine*, *Survey*, and the African-American publication *Opportunity: A Journal of Negro Life*. He took an active role in the publication of the *Birth Control Review*, providing book reviews and abstracts of his speeches for the publication. From these writings, as well as his work for the Brush Foundation and his various civic and national committees, it is clear that by the 1930s Todd was more convinced than ever before of the need for the practical social application of physical-anthropological principles (Jones-Kern, 1997, appendix A).

Despite the dramatic increase in Todd's popular, civic, and national duties during this period, Todd continued to be active in many of the professional organizations to which he belonged. In 1933, Section H of the AAAS once again elected him chairman, and five years later he reprised his stint as vice-president of the American Association of Anatomists. True to his interdisciplinary and Hunterian roots, the American Academy of Pediatrics made Todd an honorary member, and the American Association of Mammalogists elevated him to the chair of the Committee of Anatomy and Phylogeny in 1935, a post he held for the rest of his life. Perhaps the most important professional organization Todd chose to associate himself with during this period, at least in terms of his main avocation, was the newly-formed American Association of Physical Anthropology (T. W. Todd, 1938f). His prominence in the nascent organization was profoundly ironic, because he did not approve of, and even fought against, its formation.

Alas Hrdlicka had been trying to form the AAPA for many years. In 1924, he finally found enough support in the physical-anthropological community to draw up an organizational structure and list of potential members (Jones-Kern, 1997, p. 273-274). Despite the enthusiasm of many of the field's major workers, however, Todd led a successful opposition to the project based on his interdisciplinary beliefs and the feeling that the field was not yet ready for independence (Jones-Kern, 1997, p. 275). Although Todd continued to oppose official organization, by 1930 pro-organizational forces had outflanked him and officially gave birth to the AAPA. Todd still did not approve, but after some cajoling from his colleagues he decided he did not want to remain outside. Shortly before the group's first meeting, Todd became one of the last to sign on as a charter member (Jones-Kern, 1997, p. 275-283). The fact that the new association nevertheless immediately named him both to the executive board and the chair of the important Committee on Human Materials (and a few years later elected him president) was a testament to the esteem in which his co-professionals held him.

Being a member of so many professional and civic organizations often caused severe scheduling problems for Todd, and these indirectly may have enabled the AAPA to form. Because he was active in so many different groups, Todd often discovered that two or three of them scheduled their annual meetings at the same time in different places. Todd's correspondence with his colleagues often reflects his frustration with these occasions and his apologies to the groups he was unable to favor with his presence for that year. Indeed, perhaps the most significant meeting of Todd's professional career may have been one that he was unable to attend. Despite Todd's opposition to the concept of the AAPA, Hrdlicka decided to try again in 1928 using the Section H meetings in New York as a platform from which to launch the operation. To Hrdlicka's relief, Todd chose not to attend Section H that year because of previous commitments, and the drive to organize the AAPA started smoothly and with full support of the body (Spencer, 1979, p. 745-748). Hrdlicka later

remarked that he "shudder[ed] as to what would have happened [sic] had Todd been there" (Hrdlicka, 1930b).

Despite his numerous professional commitments, Todd's primary job was still that of anatomy professor and museum curator at Western Reserve. In the former capacity he expanded the school's collections even further by eventually acquiring the skeletons of more than 3,400 humans (Cobb, 1936, p. 8-14). Although Todd lost a friend and powerful professional ally with the death of Dean Hamann in 1930, Todd was well-enchanted established at this point to continue building the institution's prestige on his own, starting with Dean Hamann's memorial service. For this he brought the world famous Grafton Elliot Smith, his old friend and mentor, to the medical school to give the memorial oration. Todd's Western Reserve laboratory had already won international notice and began to draw researchers worldwide, from Scandinavia to Japan (Todd, 1930a, p. 34-36).

Despite its growing reputation as a world-class resource, the anatomy laboratory's primary function was still educational. With his many other responsibilities, Todd continued to instruct undergraduates in his innovative teaching style, and contemporaries remembered the frequent peals of laughter that issued from his freshman anatomy classes (A. Todd, personal communication, 19 August 1996). He also kept turning out top-quality graduate students. In the mid-1920s, B. Holly Broadbent became one of his earliest successful protégés, later becoming widely recognized in the field of dentistry. Carl Francis, Wilton Krogman, and W. Montague Cobb followed in the late 1920s and early 1930s, all of whom became well-respected physical anthropologists in their own right. Cobb was a particularly significant student for another reason, being the first African-American to receive a Ph.D. in anatomy from an American university. However, the quality of professionals Todd's Western Reserve laboratory generated notwithstanding, it never produced the quantity of students that such programs as Hooton's Harvard physical-anthropology department did. Just in terms of Ph.D.s, for example, Hooton had produced nine in physical anthropology by the time of Todd's death in 1938, and many more in the years to come (Spencer, 1981, p. 361), while Todd's anatomy program produced only three (UMI ProQuest Digital Dissertations). There were several reasons for this, not the least of which were the twin facts that Todd's was still essentially an anatomy (not strictly physical anthropology) lab, and the number of graduate students he could accept into his program was limited (A. Todd, personal communication, 19 August 1996). Furthermore, because of his essentially interdisciplinary scientific nature, many of the students he trained either became medical doctors or eventually gravitated to other fields for their terminal degrees (Krogman, 1939, p. 177). However, the main explanation of both the high quality and low quantity of Western Reserve anatomy Ph.D.s, was probably the exceptionally demanding nature of Todd's program (Cobb, 1936, p. 8-14; A. Todd, personal communication, 19 August 1996).

As previously discussed, Todd had extremely high scholarly standards. He kept an almost impossible schedule himself, and he expected his students to work hard and long hours as well. He was extremely intolerant of sloppy work, and his stern reprimands were quite discouraging to those students who repeatedly brought these dressing-downs upon themselves. For example, Arthur Todd's wife Dora, a former lab assistant for Professor Todd, remembered herself and others being driven to tears by his corrections (A. Todd, personal communication, 19 August 1996). In addition, Todd held a sink or swim philosophy regarding his graduate students. Cobb recalled that when he first appeared at

Western Reserve, the secretary introduced him to the staff and told him to go anywhere and do anything he wanted in the lab. He did not even meet Dr. Todd until several days later, and even then his future mentor only inquired as to his progress and told him his Ph.D. committee would meet in two weeks to determine his official program. Cobb settled into a busy schedule of his own choosing, and his program developed out of the interests he discovered in his first days there (Cobb, 1981, p. 518-519). Two years later at his graduation, Todd informed Cobb that he had decided in the first two weeks whether or not Cobb was going to get the degree. "You were left strictly alone to see if you could take care of yourself," Todd explained, "because a fellow cannot very well direct others if he cannot take care of himself" (Cobb, 1981, p. 519). Those students who passed Todd's muster won his wholehearted support, and in turn became devoted protégés and talented anatomists and anthropologists.

His students were productive as well. By the time Todd celebrated his 25th anniversary in the Henry Wilson Payne Chair, his Western Reserve anatomy department had produced 475 publications (Western Reserve University, 1937). Reflecting the diverse interests of "The Chief," these pieces were extremely eclectic in subject matter. A number addressed Todd's main area of skeletal anatomy, including papers on bone calcification, growth, shrinkage and weight; ossification and epiphyseal union in humans and guinea pigs, age changes in the pubis, scapula and temporal bones; dento- and craniofacial growth in humans, apes, and hyenas; the vertebral column, the pelvis in humans and apes, and clinical papers on the hand and amputations. His students' papers dealt with a number of other areas as well, including the muscles and vascular supply of the foot and leg, growth of the eyeball and cerebral cortex, the autonomic nervous system, the digestive tract, comparative myology, tissue respiration and the ovulatory cycle, allergies, and even child psychology. These papers, even when Todd was not officially coauthor, usually came into being under Todd's close editorial help and supervision. Many of them, particularly the epiphyseal union papers, became the standard treatments of the subject (Krogman, 1939a, 1951).

Although his students were prolific in their own right, Todd wrote or cowrote close to half of the nearly 500 items produced by the anatomy lab during his tenure. The years from 1928 to 1938 were his most prolific yet, and accounted for more than half of his published works (Krogman, 1939a; Jones-Kern, 1997, appendix A). Some, like his papers on bone changes after amputation, harkened back to his surgical and clinical roots. Also clinical in nature were his many articles (coauthored with Wilhelmine Kuenzel, his chief day-to-day assistant) on the digestive tract, most of which Todd later compiled to produce *Behavior Patterns of the Alimentary Tract*, his third book, in 1930 (A. Todd, personal communication, 8 June 1995). Todd's writings during this period also maintained his tradition of eclecticism. Various papers from his pen appeared on laboratory techniques, the eyeball, the tonsil, the vertebral column, mineral density in bone, vitamin D, the hyena, and epiphyseal union in ungulates and sirenias. As his professional stature increased, textbook editors called upon Todd to write chapters about the heart, respiratory system, and skeleton (Krogman, 1939a; Jones-Kern, 1997, appendix A).

Of greater long-term significance to anthropology than these were the last of Todd's race papers, published from 1928 to 1930. Todd and his assistants had spent nearly a decade cataloging the general morphological similarities, differences, and distinguishing characteristics of European and African "stocks" (Todd did not

like to use the term "race" except as a reference to humanity in general) in the American population. Although most of these focused on skeletal differences, Todd also produced several papers on external body measurements and the quantitative comparison of skin color. All of these were in the oldest tradition of American physical anthropology: discovering the inherent differences between the various types of mankind. By the late 1920s he was ready to summarize his findings; and the results surprised even Todd (Jones-Kern, 1997, p. 355–365).

Because most physical anthropologists until the 1940s were typological in outlook, many felt that the primary goal of the field was to find and describe these essential differences so that they could efficiently sort various races, usually along hierarchical lines. This concept is extremely important in understanding both the nature of the race-related papers printed at this time and the significance of Todd's 1929 article for *Human Biology* entitled "Entrenched Negro physical features" (T. W. Todd, 1929b). By contemporary standards, even the title sounds vaguely prejudicial. However, in its time this article was a blow against the racism then prevalent in the field. In his attempt to find those essential stock-linked differences unaffected by mixture of Americans of African and European heritage—"entrenched physical features"—Todd categorically dispensed with most of the traditional differences that were taken to be "common knowledge" at the time. Cranial capacity, head shape, pelvic measurements, and many other metrics previously used to discriminate (in both senses of the word) between White and Black people Todd showed to be highly variable and overlapping to an extent that shocked even himself. About the only physical features that he found to be relatively unaffected by "hybridization" were a few facial features, such as the nose and the lips. Along with Melville Herskovits's (1928) book on African-Americans published the year before, this article challenged a century's worth of physical-anthropological assumption (Jones-Kern, 1997, p. 359–363).

This is not to say that Todd was no longer a typologist. He continued to believe that "purer" stocks—such as West Africans—exhibited more distinct essential characteristics that required study and definition (T. W. Todd, 1929b, p. 68–69). Yet with this paper he displayed the weakening of an earlier commitment to a strong typological position, and more significantly, he broke his previous silence on the social implications of physical differences. In the *Human Biology* article, and then more forcefully in an article for *Medical Life*, Todd spoke out against the use of physical differences toward hierarchical ends: a physical difference did not imply inferiority or superiority (T. W. Todd, 1929a). Cobb, Todd's African-American student who had experienced the racism prevalent in the field at the time, later extolled the groundbreaking nature of these articles (Cobb, 1936, p. 8–14; Blakey, 1987, p. 15–24; Rankin-Hill and Blakey, 1994, p. 77–81). After nearly ten years of research on the subject, Todd became one of the very first physical anthropologists to challenge the scientific racism that had been the field's defining characteristic (Jones-Kern, 1997, p. 355–378).

These and the rest of Todd's above-described research were of varying degrees of scope and significance. However, most of Todd's work during this period—and arguably his most important—grew directly or indirectly from his Brush Foundation research. Some of this research focused on birth control, including work that later resulted in the first accurate analyses on the timing of ovulation in humans. However, most dealt either directly or indirectly with the problem of human growth and development. Many of these publications introduced and

reinforced new theories on the topic, and some were still standard works at the end of the twentieth century.

Todd's growth publications displayed a characteristic diversity. A cursory glance over the titles encompassed by this category reveals articles that touch on the subjects of health, physiology, nutrition, endocrinology, osteology, heredity, psychology, dentistry, and comparative and skeletal anatomy (Krogman, 1939a, p. 178–186). Todd also edited and coedited books on general growth topics. His assistants expanded some of this research into significant work in its own right, such as studies that led to the recalibration of the Rorschach "ink blot" test and the rejection of the idea of a supposed "problem brain wave" in children (Behrents, 1984, p. 24–32). Todd's most significant personal contributions in the area of growth, however, concerned dental and skeletal anatomy (Krogman, 1939a, 1951; Hans, Broadbent, and Nelson, 1994, p. 598–603; Nelson, Hans et al., 1995).

The comprehensiveness of Todd's scientific philosophy paid great dividends in his dental growth contributions. As might be expected of a gross anatomist, Todd introduced to orthodontics the idea that researchers should consider the entire growing organism when examining problems in the dento-facial complex. Along these lines he drew attention to the relationship between orthodontic development and bone density and mineralization elsewhere in the body. As might be expected of a comparative anatomist, he brought the study of other animals into his examinations of human jaws and teeth. Thus, he considered jaw growth in thyroidectomized sheep in the study of the problem of jaw growth in humans, and he examined the temporomandibular joint in carnivores, herbivores, and non-human primates for insights into its manifestation in humans. One of his most significant contributions to orthodontia involved both gross and comparative anatomy. From his studies on anthropoid material and Brush participants, Todd discovered the close correlation that existed between tooth eruption and epiphyseal union, a correlation that his colleague Broadbent further established and tied to pathological problems (Krogman, 1951, p. 679–683).

Another significant contribution by Todd to dentistry was manifested in the person of B. Holly Broadbent. The anatomical training Broadbent received under Todd's tutelage in part enabled him to become one of the premiere orthodontic researchers of his generation. In 1932, Todd largely retired from extensive dental research and passed his mantle in this area on to his former student. With an effusive and generous flourish that was typical of Todd, he added that this mantle "even now . . . has shrunk to but a scantling through the vigorous growth of the truly orthodontic shoulders upon which it has fallen" (T. W. Todd, 1932b, p. 799). By this time, Todd felt that orthodontics had passed its "preliminary analytical stage" (Krogman, 1951, p. 679) and had become a scientific discipline in its own right—a designation that he ironically never was willing to bestow upon his own passion of physical anthropology (Krogman, 1951, p. 679–680).

Although his dental and orthodontic work was very important, perhaps the most significant and enduring scientific contribution of Todd's Brush Inquiry research was the fundamental work he performed on bone growth and ossification. From the examination of hundreds of thousands of radiographs produced by the study, Todd discerned a definite pattern of bone maturation that applied to all social and racial groups. This was the metric-independent yardstick for which he had been looking. Todd did not completely discount the importance of chronological age in growth, but rather insisted that biological age was an equally important indicator, particularly in cases like the differences

in the timing of growth between boys and girls—differences that he also discovered and quantified. He wrote only two of the definitive epiphyseal union papers produced by the study (on the clavicle and the dens of the epistropheus), but all of the other groundbreaking articles produced from his lab bore his imprimatur from the initial research stage to the final editing. Other investigators thoroughly affirmed his once-controversial theory of “bone age” as a yardstick of growth and have accepted it ever since (Krogman, 1939a, 161–173; 1951, 679–687).

The culmination of these bone-age studies and papers was the 1937 publication of Todd's most important book, *Atlas of Skeletal Maturation: Hand*. Ten years in the making and intended to be the first in a series of books covering many different parts of the body, Todd's *Atlas* used the radiographs from his Brush Inquiry studies to demonstrate the optimal pattern of epiphyseal union in the bones of the hand. This volume, together with its 1944 revision and the other bone maturation studies produced by the Inquiry, was the basis of what became known as the Brush Standard of skeletal maturation (T. W. Todd, 1937a). Used by growth specialists, clinicians, pediatricians, radiologists, and forensic examiners around the world, the Brush Standard and the Brush Inquiry that developed it inspired other major longitudinal studies in the following years. The most important of these—the “Denver,” “Berkeley,” “Fels,” and “Harvard” studies—confirmed Todd's principal conclusions and their standards have become an important part of the literature (Tanner, 1981, p. 320–323). Significantly, however, Todd's insistence on examining only the healthiest children available made the Brush Standard child somewhat taller and earlier maturing than all subsequent standards over the next 55 years (Garn, 1981, p. 524). After almost 70 years, the current literature continues to cite the *Atlas of Skeletal Maturation*, and although many consult others, the “Brush” remained the most extensively used standard at the end of the twentieth century (based on the relative frequency of citation in standard science and social science citation indices).

The almost obsessive devotion and untiring research into the issue of improving human health of which his *Atlas* remains a testament was poignantly ironic when contrasted with the deteriorating state of Todd's own physical condition during this period. As early as the early 1920s, Todd suffered from migraine attacks so severe that he was forced to stay home all day with the blinds drawn. As his responsibilities began to heap up from the mid-1920s on, Todd pushed himself ever more relentlessly and his health began to suffer even more (A. Todd, personal communication, 19 August 1996). By the late 1920s he had developed a duodenal ulcer and a spastic colon (Cobb, 1959, p. 236). Although he characteristically used both of these conditions as research opportunities, and indeed claimed to have cured the ulcer himself by drinking vinegar and baking soda, he was never really completely well after 1931. In November of that year, in addition to his other maladies, Todd contracted a serious case of phlebitis that hampered him even further (A. Todd, 1988, and personal communication, 19 August 1996). Todd's health was so poor that his wife patiently but persistently insisted that her husband take the unusual step of going to Muskoka for a winter vacation. He eventually agreed, remembering his childhood and hoping that “the country air would cure” (D. Todd, personal communication, 9 September 1996). While Waite (1946, p. 408) claimed that during this period Todd frequently left his classes to assistants to teach so he could conduct his research, Arthur Todd insists that

almost all of the classes he missed were the result of his steadily worsening health (A. Todd, personal communication, 8 June 1995). Illness affected Todd's other duties as well. Beginning in 1930, Todd's professional correspondence began to mention his poor health occasionally, and usually apologetically, as a way of explaining unexpected delays (Hrdlicka, 1930c; T. W. Todd, 1931a, 1931b). For a man as intensely private and not prone to excuse-making as Todd, such statements were highly unusual. Despite these setbacks, though, Todd continued to keep up his hectic schedule as best he could, taking on additional responsibilities whenever they arose.

His family continued to be a great source of pride in his later years, even though none of his children followed precisely in his footsteps. Arthur, his oldest, studied history and pre-medicine at Harvard, but became a successful businessman upon graduation (A. Todd, personal communication, 8 June 1995). His son Donald also went to Harvard where Hooton personally tutored him, although the elder Todd despaired that “the young beggar gets no enthusiasm yet for the cultural aspects” (T. W. Todd, 1938c). His daughter Eleanor Margaret (“Toby”) enrolled at Smith for the fall of 1938, and this left the Cleveland Heights home alone to T. Wingate and Eleanor (“Nell”) for the first time since they moved into it. There was little time to enjoy their new-found domestic solitude. Nell herself was extremely active in her work for the Cleveland orchestra and the promotion of music in the area, and as always, Todd was very hard at work (A. Todd, personal communication, 8 June 1995).

By 1938, Todd was busier and more infirm than at any time in his career. In March the AAPA elected him president, an honor he accepted despite his reservations about the efficacy of the group. He characteristically seized the reins with both hands. A long-simmering dispute over American representation at an international conference on the standardization of anthropometric measurements was the main issue on the table when Todd assumed office, and Todd handled it with his unique blend of executive fiat and diplomacy (Jones-Kern, 1997, p. 292–300, 340–343). His main official task as the year drew to a close was the plan to celebrate Ales Hrdlicka's seventieth birthday with a banquet and a *Festschrift* devoted to his colleague. The AAPA wanted to dedicate the entire twenty-fifth volume of the *AJPA* to America's foremost physical anthropologist, with special articles commissioned for the occasion from the world's leading authorities. Among the many important articles published in the *Festschrift* would be a tribute and obituary for T. Wingate Todd.

Despite his worsening health conditions, the family's summer trip to Muskoka in the summer of 1938 was not as restful or relaxing as usual, as Todd was intent on spending much of his free time in the strenuous activity of digging a horseshoe pitch (M. Gaylord, personal communication, 26 May 1995). The teaching, departmental, and professional loads the following fall put an even greater strain on him than usual. On 27 December, after a day of work during which he sent out letters coordinating the upcoming Hrdlicka celebration and had another extremely heated argument with Frederick Waite over school policy, Todd suffered a series of three heart “spells” (Kuenzel, 1938). Rather than go to the hospital, he decided to go to bed. Very early on the morning of the 28th, Todd woke up his wife with complaints of severe chest pains. As Eleanor Todd called a doctor, Todd went to his daughter Margaret's room and woke her up (she had come home from Smith for the holidays). He briefly recovered from the pain and sat on the edge of her bed, voicing regret that he would not be

able to take advantage of the recently-purchased house at Muskoka or its new horseshoe pitch. By the time his wife got off the telephone with an unresponsive family doctor, Lester Taylor, Todd had his final coronary thrombosis and slumped beside the horrified and confused young Toby. He was dead before the ambulance carrying him reached the hospital (M. Gaylord, personal communication, 26 May 1995 and 22 July 1996).

The family held a private funeral on 30 December, followed by a public memorial service at 3:30 p.m. on 15 January, 1939, his birthday (Kuenzel, 1938; Krogman, 1939b). Staged at the Amasa Stone Chapel on the Western Reserve campus, the tribute included resolutions and testimonials from a number of people, including representatives from the School of Medicine, the Graduate School, the School of Dentistry, the Brush Foundation, the Academy of Medicine, the Cleveland Health Council, and the City of Cleveland. Movements from string quartets by Beethoven and Brahms and organ selections provided the musical interludes, and the original poem "Another Tree is Down" graced the back cover of the program. The next to last page bore but a single quotation: "The bowman hitteth the mark, as the steersman reacheth the land, by diversity of aim," a succinct reminder of "The Chiefs'" interdisciplinary nature (Anonymous, 1939). Those who knew Todd well said it was a moving and fitting tribute to the man whom his family had recently interred "on British soil" in the small hamlet of Foot's Bay near his beloved Muskoka retreat (Krogman, 1939b).

Despite the severity of his health problems, Todd's death at 53 was a tremendous shock to his family and colleagues. Telegrams and tributes came to his widow from all over, and obituaries for Todd appeared in numerous journals in many fields, including dentistry, anatomy, medicine, physiology, cultural anthropology, and surgery. His students were particularly devastated by their loss, and months later were still remarking to each other on the difficulties they were experiencing because of it (Krogman, 1939b). Journals continued to print articles under his name until 1940, and texts by his students and the Brush Foundation bore dedications to him in the following years (Cobb, 1941; Krogman, 1941; Simmons, 1944). When the AAPA celebrated its twenty-fifth anniversary in 1955, many of the reminiscences printed in the *AJPA* fondly recalled Todd's personality and influence (American Association of Physical Anthropologists, 1956, p. 349-364). His widow expressed the consensus opinion of nearly all of the tributes to Todd most succinctly in a letter sent to Hrdlicka soon after her husband's death: "But into his short life was crowded a century of endeavor, inspiration and good will" (E. Todd, 1939).

Sentiment over Todd's legacy was not entirely unmixed, however. Fellow professors such as Frederick Waite were glad to be liberated from his (perceived) meddling and excessive attention to extracurricular activities. After Todd's death, the University changed school policy so that the chairman of the anatomy department could never again concurrently head the Brush Foundation (Waite, 1946, p. 450). Even within the Brush Foundation Board of Directors, there was an expressed implication that Todd had made the organization subservient to his own personal agenda and research interests during his tenure as chair (Brush Foundation Board, 1940b).

Perhaps the most telling example of the complex mixture of respect and beleaguered tolerance some of Todd's colleagues bore toward him is in the original version of the letter of condolence that Ales Hrdlicka sent to Eleanor Todd on January 11, 1939.

Apologizing for being unable to attend the memorial service, Hrdlicka added:

But I will be with you in thought, and with the great regret that such a man and worker was so soon taken away from us. I have years ago suffered a similar loss in the death of my splendid wife, and so I know what you are passing through. But there will remain to you the great and sustaining solace that you have lost one whom everybody has loved—and honored. (Hrdlicka, 1939)

The words "loved and" were struck through in the draft in Hrdlicka's files.

Brilliant, enthusiastic, hardworking, charming, literate, and usually diplomatic, Todd was also a man of strong opinions and a forceful personality. His commitment to broad investigation and interdisciplinary study made him one of the last great comparative anatomists and marked the end of an older scientific era in an age of increasing scholarly specialization. Yet at the same time, his lifelong devotion to the problems of growth and development, combined with his boundless energy and commanding executive style, resulted in a prolific outpouring of significant research and a new understanding of such problems as somatic development and race. These efforts, and Todd himself, thus played a crucial role in the development of American physical anthropology into a fully-fledged profession and modern field of scientific inquiry.

Epilogue: T. Wingate Todd in Historical Perspective

Although scholars of physical anthropology have paid much more historical attention to the periods before and after, the years from 1900 to 1940 were far from static or insignificant in the discipline's development. On a professional level, it was precisely this period of time during which the field moved from the status of avocation to vocation, when its literature became firmly established as a self-conscious and coherent entity, and when its practitioners coalesced from a handful of independent investigators into a professional community. Moreover, this era also witnessed the beginning of physical anthropology's transition from advocacy to objectivity—from an hybrid quasi-social science with strong leanings toward practical application to a more truly biologically-oriented and dispassionate academic area of study.

The early twentieth century was also a crucial period in physical anthropology's theoretical and methodological transition to modern biological anthropology. Although the many changes loosely referred to as "the new physical anthropology" were not complete until the 1950s and later, most had begun before 1940. For example, somatology's old primary focus of comparative racial and ethnic anatomy remained its strongest single component during the pre-World War II period, but numerous new areas of investigation (for example, human origins, primatology, growth studies, dental anatomy, functional morphology, human genetics) began to vie for attention by the 1920s and 1930s. Similarly, while physical anthropology played no significant role in the development of population biology and the evolutionary synthesis in the 1930s and 1940s (and did not officially begin to assimilate these theories until the 1950s), by this time some of its leaders had already begun to move away from its century-old devotion to strict typology and racial formalism. Many of the major methodological developments credited to the second half of the twentieth century also originated in the first. Human serology and histology, advanced statistics, hypothesis-testing, and the decline of traditional anthropometry (to

name only a few) all trace back to researchers working in the days of "the old physical anthropology." Any history of these developments is incomplete without due attention to the pioneers of the early 1900s, including T. Wingate Todd.

In many ways, the figure of Todd is an ideal lens through which to view this formative period of modern physical anthropology. Unlike his older peers (such as Ales Hrdlicka and Earnest Hooton) who largely exemplified the "old physical anthropology," or his younger colleagues (like M. F. Ashley Montagu) who represented important coming changes, Todd stood as a Janus among his peers. His often unorthodox views of the field embodied at once numerous elements of its past and future, as well as the dynamics of its evolution. A key figure in the emerging discipline, Todd more than any of his contemporaries personified the full spectrum of physical anthropology's transition to modern biological anthropology.

Professionally, in accordance with physical anthropology's more traditional roots, Todd favored a medical-style training regimen and the practical application of physical-anthropological knowledge toward the betterment of society. Along the lines of the latter, his unorthodox and reformist eugenic beliefs (in the form of the Brush Foundation) became increasingly anomalous in a field populated with researchers who either adhered to mainstream eugenics or distanced themselves from the movement entirely. Perhaps the most obvious example of Todd's older view of somatology was his opposition to Hrdlicka's formation of the AAPA. He saw no reason for professional separation of the discipline from anthropology and anatomy, and waged an initially successful battle against the organization. At the same time, however, Todd also strove toward a significantly higher standard of objectivity in somatological research and railed against amateurism in the work of his peers. His prolific and frequently unimpeachable scholarly work was an important part of the nascent field's literature, and was still actively cited at the end of the twentieth century. Although he thought the formation of the AAPA premature, he nevertheless became one of the group's charter members and most active early leaders. Along with Hrdlicka and Hooton, Todd was one of the three most respected and significant members of the young American physical-anthropological profession.

On the level of theory and practice, Todd represented an even more dynamic example of his field's transitional nature. True to later changes in the larger physical-anthropological community, Todd's initial, largely traditional focus on racial and skeletal anatomy gave way to more modern studies of growth and functional anatomy. Similarly, in theoretical matters Todd held an old-fashioned adherence to typological and orthogenetic thinking that he nevertheless alloyed with more modern scientific thought. Along with Franz Boas, Todd staked out a middle-ground between the biological determinism of the past and the population biology of the future with his emphases on variation, "family-line" inheritance, and environmentalism. Methodologically, Todd was a pioneer in the anthropological use of many new techniques, including x-ray technology, fluoroscopy, statistics, and hypothesis-testing. Reflecting later changes in the discipline, he moved from a standard anthropometric orientation early in his career to an ultimate rejection of the practice as sterile and largely meaningless in the years preceding his death. Perhaps even more importantly, the process of aging skeletons by examining the pubis and epiphyseal union patterns that Todd almost exclusively established is still used by physical anthropologists today. It is for this, and for the massive Hamann-Todd osteological collection he

assembled, that Todd was most recognized at the end of the twentieth century.

Todd died before he could witness the sweeping changes that reshaped the field in the 1940s and 1950s, but his presence and impact on American physical anthropology lingered in both his work and his students. Wilton Krogman carried on Todd's growth research work and became president of the AAPA eight years (almost to the day) after Todd's death. Moreover, seventeen years after the meeting that eulogized Todd and quashed a resolution against racism, the 1956 convention of the AAPA overwhelmingly passed a resolution moved by W. Montague Cobb stating that its members "affirm that they know of no evidence that any group is inferior to any other group by virtue of race." Historians have grossly underappreciated Todd's seminal role in this wholesale shift in attitude of physical anthropology. Not only did he conduct some of the most important early research that eviscerated old racist anthropological arguments of typological ethnic differences—work continued by his students after his death—he integrated the field by fiat in his mentorship of Cobb. Symbolic of the great changes which Todd initiated in this area, Cobb was serving his second vice-presidency of the organization when he proposed the resolution against racism (his first was from 1949 to 1950), and he became its first African-American president soon thereafter (American Association of Physical Anthropologists, 1956, p. 367).

Both Cobb and Krogman continued to be important voices extolling the Todd perspective in the rapidly-expanding profession, and over the course of their careers they witnessed many changes in the field reminiscent of their early training. As late as 1985, Cobb (*in* Rankin-Hill and Blakey, 1994, p. 80) commented:

And one of the most remarkable things about Todd, was he did so much in such a short time ... and I can say from this perspective, only now, are the fruits of Todd's work being realized.... The Todd laboratory was way ahead. It was interdisciplinary already. Of course now they [physical anthropologists] are coming around to it.

Thus, Todd's characteristic interdisciplinary emphasis was more than a reflection of the field's past, it presaged developments far into its future. Similarly, Todd's seemingly old-fashioned model for physical anthropological training has experienced a resurgence of sorts in the past 35 years, with some leading biological anthropology graduate departments utilizing the facilities and courses of allied medical schools as integral parts of their degree programs. His osteological collection—which fell into almost utter disuse and near destruction in the years following his death—experienced a dramatic renaissance with its rehabilitation at the Cleveland Museum of Natural History, where it stands as a world-class scientific resource (Jones-Kern, 1994). Late in the twentieth century, articles based on Hamann-Todd collection research appeared in scholarly journals on average twice a month—about the same frequency that researchers continued to cite Todd's writings. In these and many other ways, both Todd and "the old physical anthropology" of the early 1900s continue to influence the modern field, and thus deserve considerably more historical scrutiny than they have received.

T. Wingate Todd's place in American physical anthropology, then, is considerably more profound than previously recognized. Ales Hrdlicka deserves the lion's share of credit for the organization of the field, and Earnest Hooton led everyone else by far in the production of the following generation's practi-

tioners. Todd contributed significantly in these areas as well, but played a far more consequential part than either of these men in the discipline's scholarly development. During his own time, his peers (including Hooton and Hrdlicka) recognized him as one of the most important men in the field, and deferred to the quality of his work. His voluminous written output comprised a significant portion of the contemporary literature, and his contemporaries rarely contradicted it. In more diachronic terms, he led nearly all of his peers in the eventual turn the field made away from the ethnic focus of its racialist roots and the biological determinism of the eugenics movement. Furthermore, he anticipated the profound theoretical and methodological changes that eventually put physical anthropology on its present scientific footing. His research collections are the largest of their kind in the world, and still quite actively used by contemporary researchers. The fact that many of Todd's publications from as early as the 1920s are still considered standard works in a field that changed so dramatically after his death attests to the fact that he was in many respects ahead of his time, and one of the most significant figures in American physical-anthropological history.

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ANALYSIS OF DIATOM COMMUNITIES IN AN ACID-MINE-DRAINAGE-IMPACTED SUBWATERSHED IN SOUTHEASTERN OHIO

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ABSTRACT

Acid mine drainage (AMD) impacts numerous streams worldwide. During June of 2000, 18 stream segments located within the Black Fork subwatershed in southeastern Ohio were sampled for diatom flora and critical environmental parameters. This area has a history of prolific coal mining and many of the region's lotic systems are inundated with AMD. In this region, many of the abandoned mines have been reclaimed using various techniques. The goal of this study was to determine if diatom assemblages could provide evidence of the progress and effectiveness of reclamation activities with respect to biotic integrity of aquatic systems. Through the cross-referencing of various exploratory techniques three distinct groupings of sites were depicted, each containing similar relative abundances of important diatom taxa. Group I sites were heavily impacted by AMD and were dominated by *Eimotia exigua* (Brébisson ex Kützing) Rabenhorst. Group II sites were moderately impacted by AMD and had diatom assemblages of *Achnanthes minutissimum* (Kützing) Czarnecki, and *Brachysira vitrea* (Grunow) R. Ross in B. Harley. Group III sites contained relatively unimpacted headwater regions in the subwatershed with diatom assemblages dominated by *A. minutissimum*. The diatom assemblages were useful in identifying certain sites that prior to this study were thought to be major contributors of AMD, but yielded taxa characteristic of intermediate conditions, suggesting that these sites fluctuate in water chemistry throughout the year. The unique diatom assemblages in these intermediate, oscillating streams (Group II) pinpointed cryptic pollution sites with a greater degree of accuracy than environmental parameters alone.

Introduction

Coal mining has been a vital industry to the Appalachian region since the early 1800s. The coal-mining process can lead to a variety of environmental impacts including hydrogeochemical effects, subsidence, and mine gas emission (Banks et al., 1997). While all of these examples represent serious dilemmas, the predominant environmental problem associated with coal mining is acid mine drainage (AMD). AMD is defined as runoff of a dilute solution of sulfuric acid and iron sulfate in the ferrous and ferric form (USEPA, 1983). This drainage results from the exposure of mine subsidence and spoils, which contain substantial

quantities of pyritic minerals (FeS_2), to oxidation (both abiotic and biotic). AMD can have a negative effect on the diversity of aquatic ecosystems due to toxicity from increased hydrogen ion activity, dissolved metals, and an influx of metal precipitates which degrade available habitat (Herricks, 1977; Leatherman and Mitsch, 1978; Mulholland et al., 1986; Wieder et al., 1990; Skousen et al., 1994; Keating et al., 1996; Planas, 1996; Verb and Vis, 2000, 2005). There are an estimated 16,090 km of AMD-impacted stream systems in the Appalachian region (Dugan, 1975; Starnes, 1985).

Despite reductions in species richness in AMD-impacted systems, a variety of organisms can be employed as biological

indicators in such investigations. Of these organisms, the algae, particularly diatom assemblages, have several advantages over other organisms as biomonitors because they are abundant and have cosmopolitan distributions within a watershed (i.e., Lowe and Pan, 1996; Stevenson and Pan, 1999). Furthermore, the diatom communities are excellent biological indicators of surface water acidity and have shown promise in the evaluation of AMD remediation (Battarbee et al., 1999; Verb and Vis, 2000, 2005).

The goals of this investigation were to: 1) determine the influence of AMD on the benthic diatom assemblages within a small subwatershed and, 2) explore the amount of resolution the diatom assemblages provide when assessing the remediation success of abandoned coal mines within a small subwatershed.

Methods

The sedimentary rocks of the Moxahala watershed were laid down from the Mississippian to the Permian periods and consist primarily of sandstone, shale, limestone, and Pennsylvanian-age coal. There are also glacial-outwash deposits of clay, silt, and gravel of Quaternary age. The Moxahala drainage basin has an average pH of approximately 6.0 in its headwater regions, although near its confluence with the Muskingum River the pH decreases to 4.5 (Eberhart, 1998; Kocsis, 2000). The Moxahala watershed suffers from a high degree of both chemical and sedimentation pollution and is currently one of the most highly AMD-impacted hydrologic units in the state of Ohio (USDA, 1985; Eberhart, 1998). These studies indicated that there were contaminations of AMD in approximately 60 percent of the watershed's 267 km of tributaries and 132 km of excessive sedimentation. Coal was mined in approximately 68 km² of the watershed (USDA, 1985). The Black Fork subwatershed represents one third of the total Moxahala watershed (~78 km²) and has three main contributors: Dry Run, Ogg Creek, and Bennett Run. Black Fork provides approximately 25 percent of the total flow to Moxahala Creek. However, it is the least contaminated of four major tributaries discharging into Moxahala Creek, contributing between 15 and 20 percent of the total iron and sulfate loading (Eberhart, 1998; Kocsis, 2000). The Ohio Department of Natural Resources-Division of Mines and Reclamation (ODNR-DMR) determined that the Black Fork subwatershed would be the focus of various reclamation efforts (e.g., wetlands) and a detailed watershed analysis because it has the greatest potential for full recovery (Kocsis, 2000).

The Muskingum Mining Company mined 10 km² of No. 6 coal prior to 1956 from the Misco Mine. The company deposited two large refuse piles (Misco gob piles) on both banks of Bennett Run. Since the Misco gob piles represented the primary sources of AMD in the Black Fork subwatershed they were partially reclaimed in 1990. The reclamation efforts included excavation and regrading of one gob pile along with the stifling of 16,820 m³ of burning coal refuse before the pile was capped. Topsoil was replaced and the site was revegetated. The second burning (9,175 m³) refuse pile was left unreclaimed due to a lack of funds (Kocsis, 2000).

The second major AMD source in the Black Fork subwatershed arises from an underground mine seep near Tropic, Ohio. In 1994 the ODNR-DMR designed and constructed a treatment wetland (Tropic Wetland). The AMD seep is funneled into an anoxic limestone drain (ALD) and then travels through a pipe where it discharges into a sedimentation pond. Subsequently, the water is directed into one of twelve wetland cells. Each cell has a base of peat mixed with lime in order to provide suitable

substrate for bacterial colonization and increased alkalinity. Corrugated fiberglass sheets separate each cell and the cells empty into collection channels, which then discharge into one of two outlets to Black Fork (Kocsis, 2000).

Physical and chemical analysis

Eighteen preselected sites were visited in June 2000. These sites represented permanent sampling stations for the Black Fork subwatershed investigation initiated by ODNR-DMR (Table 1 and Figure 1).

At each sampling site, a 20-m stream segment was measured for maximum wetted width at three randomly determined locations. The average thalweg depth (deepest part of channel) was calculated every 2 m along the 20-m transect (11 total measurements). Specific conductance, pH, and temperature were measured at each site using handheld probes. Stream water was collected at each site in 1000 ml, 500 ml, and 250 ml containers for water chemistry and placed on ice for transportation. The 1000-ml and 500-ml samples were then shipped to the ODNR-DMR analytical laboratory in Cambridge, Ohio for analysis of pH, total acidity, total alkalinity, total suspended solids, sulfate, chloride, total calcium, total magnesium, total sodium, total potassium, total iron, total manganese, total aluminum, and hardness. Within eight hours of collection, stream water from the 250 ml container was analyzed for turbidity (using a Hach 2100PTM turbidity meter), and water samples were filtered using Whatman GF/F μ m filters for nitrate (NO₃-N), soluble reactive phosphorus (SRP), and sulfate (SO₄²⁻), and 0.45 μ m filters for silica (SiO₂). These analyses were conducted with a Hach DR/890TM colorimeter with standard protocols and powder pills from Hach Company (Anonymous, 1997).

Diatom sampling and analysis

At each site, five rocks were randomly selected from a transect placed across a riffle area and a 5.0 cm² area on each rock was scraped for periphyton by securing a rigid rubber O-ring, scouring with a stiff toothbrush, and rinsing with stream water. Material from the five scrapes was combined and a composite sample of

Table 1. Descriptions of 18 sampling locations from within the Black Fork subwatershed as defined by Kocsis (2000). AMD = acid mine drainage, ALD = anoxic limestone drain.

Station abbreviation	Description
BF1	Black Fork before entering Moxahala Creek
BF10	Whitehouse Seep before entering Black Fork
BF13	Black Fork before AMD contamination
DR1	Dry Run before entering Black Fork
DR2	Seep No. 2 before entering Dry Run
DR3	Seep No. 1 before entering Dry Run
DR7	Dry Run before merging with seeps
OC1	Ogg Creek before entering Black Fork
OC4	Ogg Creek before AMD contamination
BR1	Bennett Run before entering Ogg Creek
BR3	Discharge from burning gob pile into Bennett Run
BR9	Bennett Run before burning gob pile
BR14	Bennett Run before AMD contamination
TW0	Tropic Wetland well—before ALD
TW1	Outlet from ALD to Tropic Wetland sedimentation pool
TW2	Channel leading from sedimentation pool to Tropic Wetland
TW3	Tropic Wetland—discharge to Black Fork
TW4	Tropic Wetland—discharge to Black Fork

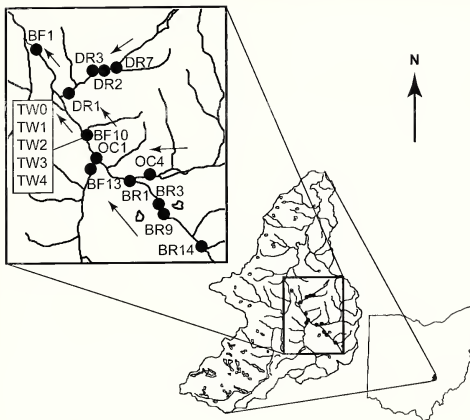


Figure 1. Map indicating the location of the Moxahala watershed in southeastern Ohio, the Black Fork subwatershed within the Moxahala watershed, and the sampling locations for the current investigation. Arrows indicate direction of water flow in the tributaries. The inset box is 5.25-km wide.

20 ml was preserved with 2.5 percent CaCO_3 -buffered glutaraldehyde for later identification and enumeration of benthic diatoms.

Palmer-Maloney counting chambers were used to determine abundances and basic morphologies of living diatoms (presence/absence of chloroplast) in each sample. Preserved diatom samples were homogenized and a 10 ml subsample was cleaned using 30 percent H_2O_2 and concentrated HNO_3 (Stoermer et al., 1995). The clean diatom sample was suspended in glass-distilled water, placed in evaporation chambers similar to those devised by Battarbee (1973), and prepared on slides using NAPHRAX. For each sampling date, 600–1000 valves were counted along 18-mm transects at 1000 \times using a BX40 Olympus microscope.

Diatoms were identified to species using Patrick and Reimer (1966, 1975) and Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b). Relative abundance, the Shannon index of diversity, density, and numerical species richness were calculated for each subsample (Magurran, 1988, p. 7–45).

Statistical analyses

Data were initially inspected for adherence to the assumptions of univariate and multivariate normality. Non-normal data were transformed using \log_{10} and $\log_{10} + 1$ to meet normality assumptions. Exploratory analyses were conducted with both species data and environmental data from each site and date to investigate the relationship of the streams based on the degree of AMD contamination. Unweighted pair-group mean average (UPGMA) cluster analyses were conducted using NCSS 2000 (Hintze, 2000) statistical software, environmental data were examined using principal components analysis (PCA) and correspondence analysis (CA) for species data using CANOCO (ter Braak and Šmilauer, 1998).

Detrended correspondence analysis (DCA) was used to determine the variation in the algal data sets. Based on the gradient lengths along the first DCA axis it was determined that canonical correspondence analysis (CCA, unimodal response model) would be the proper ordination technique to employ (ter Braak and Prentice, 1988). The patterns observed from exploratory statistics (UPGMA, PCA, CA) were compared with the results of canonical correspondence analysis (CCA) using CANOCO (ter Braak and Šmilauer, 1998) to determine if there were distinguishable groups of taxa and stream sites that could be used in classification. Through the cross-referencing of these techniques, the stream sites were partitioned into multivariate groups. CCA was conducted using abundant diatom taxa (relative abundance ≥ 0.5 percent, present at ≥ 2 sites). Environmental data were analyzed and \log_{10} -transformations applied to those parameters with skewed distributions. Those variables with high correlation coefficients ($r > 0.85$) and variance inflation factors (> 10) were eliminated (Pan et al., 1996; ter Braak and Šmilauer, 1998). The significance of the first 4 CCA axes was tested using Monte Carlo permutation tests (1000 permutations, $\alpha = 0.05$). To further test the influence and significance of important environmental variables from the initial CCA, a series of constrained CCAs were conducted along with Monte Carlo permutation tests (ter Braak and Šmilauer, 1998).

Two unbalanced multivariate analyses of variance (MANOVA) were conducted using SAS (SAS Institute Inc., 1996). Stream group from multivariate analyses was a fixed effect with measurements of the algal assemblages (species diversity and richness) and selected environmental parameters as response variables. Bonferroni (Dunn) multiple comparison tests were employed to investigate significant differences among the category types.

Results

CCA results

Of the original 22 variables measured from the stream sites, 14 were excluded due to problems associated with autocorrelation and variance inflation. A total of 105 diatom species were identified in the samples recovered from the Black Fork subwatershed. Of these, 62 taxa were included in the multivariate analyses because they had a relative abundance ≥ 0.5 percent and were present at ≥ 2 sites. Site TW0 (wetland well) contained no diatom taxa and thus was eliminated from the CCA analyses. The first four axes of the periphyton CCA were statistically significant (Monte Carlo permutation, $P = 0.02$) and explained 45.7 percent of the species variance (Table 2). The correlation between the diatoms and physical and chemical variables was highest along the first and second axes ($r = 0.69, -0.88$) and dropped in the following axes ($r = 0.53, -0.66$; Table 2). There was an influence of mine drainage along CCA axes 1, 3, and 4 (Table 2). The first axis was strongly correlated with pH ($r = -0.88$) while the second axis was influenced by temperature ($r = 0.83$; Table 2). The eight variables included in this analysis accounted for 72.7 percent of the total explained diatom species variance (Table 2). Constrained CCAs performed on these eight environmental variables revealed that two of these variables, pH and Fe, were statistically significant ($P < 0.05$; Table 3).

Site distributions and characteristics

Cross-referencing of the various exploratory techniques (i.e., clustering, PCA, CCA) was employed to determine the

Table 2. Summary of canonical-correspondence-analyses (CCA) results for the first four axes of the diatom set. λ = eigenvalue; S = percent variance explained by the corresponding axis; SER = species-environment relation; TVE = total variance explained; r = correlation coefficient between axis and influential environmental parameters. All axes were statistically significant ($P < 0.05$) as determined by Monte Carlo permutation tests (1000 bootstrap replicates).

Axis	λ	S	SER	Environmental parameter (r)
I	0.449	21.3	33.9	pH (-0.88), Fe (0.69)
II	0.193	9.3	14.7	Temperature (0.83)
III	0.156	8.7	13.9	Turbidity (0.60), Fe (0.53), Width (-0.53)
IV	0.127	6.4	10.2	Al (-0.66)
TVE		45.7	72.7	

Table 3. Constrained CCA results of environmental variables employed in the initial CCA.

Variable	Percent variance explained	Monte Carlo P -value
pH	16.9	.0010
Fe	13.6	.0070
Width	9.5	.0509
Turbidity	8.5	.0899
Temperature	7.8	.1389
PO ₄	7.7	.2008
Al	7.1	.2527
Depth	5.1	.7283

indicated three groups of sites. Due to the repetitive nature of these analyses only the results of the CCA are presented since this analysis type incorporates both the environmental and diatom data sets (Figure 2). In all analyses the composition of the three multivariate groups remained in relative agreement. Stream site variation that occurred was primarily due to the switching of site positions within each multivariate group. Group I was composed of sites heavily impacted by AMD. The stream water at these sites was the lowest in pH and turbidity (Table 4). Heavily impacted AMD sites (Group I) also had the highest concentrations of dissolved metallic ions (Al, Fe, Mn), specific conductance, and SiO₂ (Table 4). The second multivariate grouping was comprised of several remediated and unreclaimed sites, that were moderately impacted by AMD (Figure 2). These sites were moderately acidic with low buffering capacities (Table 4). Group II sites had moderate concentrations of Al, Fe, Mn, specific conductance, and SO₄²⁻ which were significantly higher than the levels found in Group III, but not Group I (Table 4). Group III was an agglomeration of three headwater sites with little to no AMD impact. These sites displayed circumneutral pH levels with low concentrations of AMD-related variables (i.e., Al, Fe, Mn). Group III sites also had the highest levels of total alkalinity recorded in this study (Table 4).

The heavily impacted AMD sites located in Group I were dominated by *Eumotia exigua*, with additional assemblage composition from *Nitzschia capitellata*, *Pinnularia subcapitata*, *Frustulia rhomboides*, and *Eumotia steineckii* (Appendix 1). Moderately impacted AMD sites contained in Group II displayed diatom assemblages containing *Achnanthyrium minutissimum*,

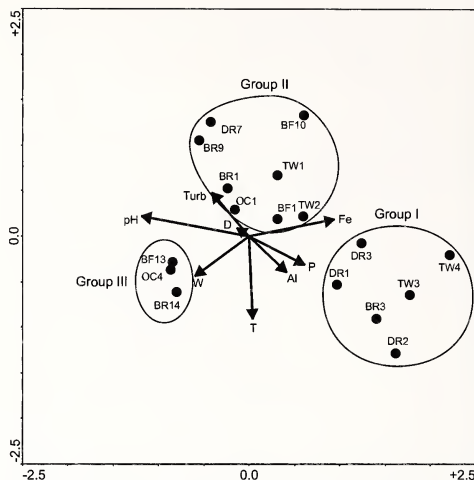


Figure 2. Diatom-based CCA biplots of Black Fork subwatershed stream sites with environmental variables represented by arrows. D = thalweg depth, P = orthophosphate, T = temperature, Turb = turbidity, W = maximum wetted width.

Pinnularia obscura, *Brachysira vitrea*, *Eumotia exigua*, and *Nitzschia inconspicua* (Appendix 1). The relatively unimpacted headwater sites (Group III) had a flora of *A. minutissimum*, *N. acicularis*, *N. dissipata*, *Planothidium lanceolatum*, and *Rhoicosphenia curvata* (Appendix 1).

Multivariate Groups I and II had levels of diatom species richness and diversity that were significantly (MANOVA: $P < 0.05$) lower than the measurements from Group III (Figure 3A, B). In addition, Group I was significantly lower (MANOVA: $P < 0.05$) than Group II in both of these measurements as well.

Discussion

CCA results

There was a clear delineation between the three multivariate groups, with little gradation between them. The influence of pH on these systems was not unexpected, given the wide range of pH values (2.7–7.2) and the importance of this variable in other lotic studies from the region (Pan et al., 1996; Verb and Vis, 2000, 2001, 2005). However, along the second CCA axis the influence of temperature was unanticipated. The lower water temperatures were predominately associated with the headwater systems in Group I, water discharging from the ALD, and many of the systems receiving AMD-contaminated groundwater (e.g., seeps). Despite the perceived importance of temperature along the second CCA axis this variable was not statistically significant when examined with a constrained CCA. The 30.6 percent of the diatom variance explained by the first two CCA axes is higher than in other lotic algal studies (12.0–21.1 percent), but the inflation of this value may be attributed to the small number of samples in this study (17 containing diatoms).

Table 4. Summary of descriptive statistics for selected environmental variables (median value with ranges) and for 17 sample sites with diatoms in the Black Fork subwatershed. Stream categories according to ordinations groups described in the text. NTU = Nephelometric Turbidity Units; SRP = Soluble Reactive Phosphorus; TDS = Total Dissolved Solids; TSS = Total Suspended Solids; * = variables used in multivariate analyses.

Parameter	Group I	Group II	Group III
Al ³⁺ (mg/l)	16.0 (1.2–212.0)	4.1 (2.3–17.3)	0.65 (0.54–2.88)
Specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$)	2735 (1020–3250)	828 (331–2300)	264 (250–298)
Fe ³⁺ (mg/l)	44.9 (13.7–645.0)	37.9 (1.91–326.0)	0.4 (0.2–0.4)
Maximum wetted width* (m)	6.0 (0.9–7.2)	2.2 (1.1–7.2)	5.7 (5.3–8.0)
Mn (mg/l)	3.8 (1.7–5.3)	1.1 (0.5–4.9)	0.2 (0.1–0.2)
NO ₃ (mg/l)	0.5 (0.1–4.6)	0.0 (0.0–0.9)	0.0 (0.0–0.1)
pH*	2.84 (2.68–3.07)	5.54 (5.19–6.42)	7.11 (6.97–7.23)
SRP* (mg/l)	0.49 (0.14–0.75)	0.26 (0.20–0.79)	0.24 (0.20–0.26)
SiO ₂ (mg/l)	30.7 (16.3–63.9)	8.6 (2.6–26.9)	5.0 (3.8–5.9)
SO ₄ ²⁻ (mg/l)	1474 (410–3013)	389 (85–1605)	31 (31–35)
TDS (mg/l)	2120 (597–4540)	628 (215–2540)	152 (148–160)
TSS (mg/l)	15 (9–97)	58 (10–184)	9 (5–10)
Temperature* (°C)	20 (16–23)	16 (14–18)	15 (14–17)
Thalweg depth* (cm)	8 (4–86)	10 (4–26)	9 (8–42)
Total acidity (mg/l)	186 (114–511)	52 (0–317)	0 (0)
Total alkalinity (mg/l)	0 (0)	8 (4–57)	85 (72–99)
Turbidity* (NTU)	3.8 (0.8–5.5)	100.4 (7.8–458.0)	11.7 (3.4–30.0)

Multivariate groups

Taxa associated with Group I are very characteristic of acidic conditions. *Eumotia exigua*, *E. steineckii*, *N. capitellata*, *P. subcapitata*, and *F. rhomboides* are all taxa that have been reported from acidic lotic conditions (Bennett, 1969; Hancock, 1973; Patrick, 1977; Kelly, 1988; Planas, 1996; DeNicola, 2000; Verb and Vis, 2000, 2005). While Group II showed moderate effects of AMD (e.g., depressed levels of species richness), sites within this grouping contained rather unique diatom taxa in the assemblages. The importance of *A. minutissimum*, *B. vitrea*, and *P. obscura* at these sites was interesting because these are the dominant taxa in lotic systems in this region which oscillate in water chemistry from acidic to circumneutral (Verb and Vis, 2000, 2005). *Pinnularia obscura* was an especially intriguing taxon given that it is often recorded as a common aerial diatom, typical of somewhat brackish water conditions (Van Dam et al., 1994; Johansen, 1999). However, several investigations report this taxon being found in a wide range of freshwater environments (Patrick and Reimer, 1966; Troeger, 1978, 1983; Pfister et al., 1979). Further investigation is required to determine if *P. obscura* is indicative of these oscillating water conditions and/or an aberrant aerial taxon being flushed into the system via surface runoff. Group III sites contained diatom taxa, such as *N. acicularis*, *N. dissipata*, *P. lanceolatum*, and *R. curvata*, that were generally intolerant of acidic conditions (Verb and Vis, 2000).

AMD pollution sources

Kocsis (2000) reported that there were four major AMD sources in the Black Fork subwatershed: Tropic Wetland (TW0-TW4), Whitehouse Seep (BF10), Dry Run (DR1, DR2, DR3, DR7), and the Misco burning gob pile (BR3). The Tropic Wetland was considered to be operating sufficiently (Fe removal and neutralization of mineral acidity) with the exception of sulfate removal (Kocsis, 2000), however, there was a definite spatial divergence between the diatom assemblages found near the ALD and where the wetland discharges into Black Fork. The two sites near the ALD discharge (TW1 and TW2) represent moderate AMD impact, but at the end of the wetland treatment (TW3 and TW4), diatom assemblages indicate these sites are heavily

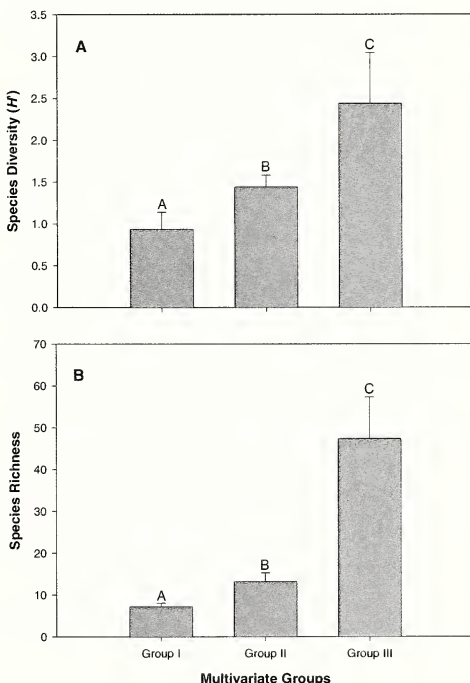


Figure 3. Mean values (+SE) for selected diatom assemblage variables. Bars with the same letters are not significantly different ($P < 0.05$).

impacted by AMD. TW3 and TW4 are dominated by *E. exigua* (73–84 percent relative abundance), a taxon prevalent in heavily impacted AMD sites of this region (Verb and Vis, 2000, 2005). It appears that the ALD is effective at raising the pH of the water discharging from it and the sedimentation pool (TW1 and TW2). It has been postulated that as this treated water moves through the wetland hydrolysis, precipitation of the oxidized Fe generates additional hydrogen ions (Kocsis, 2000), resulting in the acidic conditions and flora found at the wetland discharge points (TW3 and TW4). Furthermore, it has been noted that precipitating Fe flocc may alter the physical environment in which the diatoms reside and the same may be true for these sampling sites (Verb and Vis, 2005). However, another plausible explanation for the AMD within water discharging from the Tropic Wetland may be the intrusion of AMD-contaminated groundwater which is either bypassing or not being neutralized by the ALD and microbial processes. Nevertheless, further investigation into the hydrologic regime around and within the Tropic Wetland is needed to confirm or deny these suspicions.

The Whitehouse Seep (BF10) represented the largest flow contributor to Black Fork but was considered third on the list of AMD sources in this basin (Kocsis, 2000). However, the diatom assemblage and environmental parameters depicted this particular site within Group II, which is comprised of moderately impacted AMD sites. The dominance of the diatoms *A. minutissimum*, *B. vitrea*, and *P. obscura*, along with low levels of total alkalinity (10.4 mg/l), are indicative of intermediate AMD disturbance and perhaps oscillating water chemistry (fluctuating between acidic and circumneutral pH) (Verb and Vis, 2000, 2001, 2005).

The Misco burning gob pile (BR3), contributing < 10 percent of the flow to Black Fork, was considered one of the more severe AMD point discharges in the Black Fork subwatershed. Diatom taxa were highly indicative of heavily impacted AMD conditions with a flora dominated by *E. exigua*, *N. capitellata*, and *P. subcapitata*.

The final major source of AMD in the Black Fork subwatershed was Dry Run. In its headwater region (DR7) this tributary is only marginally impacted by AMD as indicated by its location in multivariate Group II. At DR7 the dominant diatom taxa are *A. minutissimum*, *E. exigua*, *B. vitrea*, and *N. inconspicua*, suggesting that at this site (DR7) the system may be oscillating in nature. However, after the two AMD seeps (DR2 and DR3) merge with Dry Run downstream, there was a degradation in water quality and a corresponding reduction in species richness and a rise in the dominance of *E. exigua* (50–95 percent relative abundance) in the diatom assemblages.

In conclusion, diatoms were useful at detecting and characterizing the various AMD intensities at sites throughout the Black Fork subwatershed. Furthermore, some sites that were thought to be major contributors of AMD supported a diatom assemblage that was representative of intermediate AMD (i.e., BF10). Evidence from this study provides further support that diatom assemblages are useful in characterizing AMD pollution at a variety of spatial scales (small subwatershed to ecoregion). In addition, diatoms are a useful tool in pinpointing problematic AMD-pollution sectors and may prove to be useful organisms in tracking the impacts of restoration efforts.

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Appendix 1. Mean relative abundance of dominant diatom taxa for each multivariate group of stream sites sampled in the Black Fork subwatershed.

Taxon	Multivariate Group		
	I	II	III
<i>Achnanthes flexa</i> Reimer	0.00	0.76	0.55
<i>Achnanthes minutissimum</i> (Kütz.) Czarn.	1.77	29.20	44.56
<i>Amphipleura pellucida</i> (Kütz.) Kütz.	0.00	0.16	0.10
<i>Amphora montana</i> Krasske	0.00	0.35	0.10
<i>Brachysira vitrea</i> (Grunow) Ross	0.48	9.10	0.00
<i>Cocconeis pediculus</i> Ehrenb.	0.00	0.16	1.00
<i>C. placentula</i> Ehrenb.	0.00	0.00	0.22
<i>Craticula halophila</i> (Grunow) Mann	0.00	2.29	0.11
<i>Cymbella affinis</i> Kütz.	0.00	1.85	0.52
<i>Denticula kuetzingii</i> Grunow	0.00	0.33	0.09
<i>Diatoma vulgare</i> Bory	0.00	0.16	0.10
<i>Encyonema lange-bertalotii</i> Krammer	0.00	0.00	0.20
<i>E. minimum</i> (Hülse ex Rabenh.) Mann	0.00	0.35	1.01
<i>E. silesiacum</i> (Bleisch ex Rabenh.) Mann	0.00	0.33	0.41
<i>Eumotia curvata</i> (Kütz.) Lagerst.	0.77	0.20	0.21
<i>E. exigua</i> (Bréb.) Rabenh.	71.50	5.75	0.63
<i>E. steineckii</i> Petersen	1.57	0.21	0.00
<i>Fragilaria capucina</i> Desm.	0.21	1.23	1.45
<i>F. tenera</i> (Smith) Lange-Bert.	0.00	0.00	0.43
<i>Frustulia rhomboides</i> (Ehrenb.) DeToni	5.11	0.00	0.00
<i>Gomphonema olivacea</i> (Hornemann) Dawson	0.00	0.33	1.53
<i>Gomphonema</i> sp.	0.00	0.66	0.50
<i>G. minuta</i> Agardh	0.00	0.00	0.71
<i>G. parvulum</i> (Kütz.) Kütz.	0.24	0.45	0.41
<i>Luticola mutica</i> (Kütz.) Mann	0.24	0.35	0.00
<i>Melosira varians</i> Agardh	0.00	2.08	2.48
<i>Meridion circulare</i> (Grev.) Agardh	0.00	0.00	0.95
<i>Navicula cincta</i> (Ehrenb.) Ralfs	0.00	0.20	1.15
<i>N. clementis</i> Grunow	0.00	0.68	0.00
<i>N. cryptocephala</i> Kütz.	0.00	0.51	0.53
<i>N. cryptonella</i> Lange-Bert.	0.95	0.00	1.40
<i>N. goeppertiana</i> (Bleisch) H. L. Smith	0.06	0.78	0.00
<i>N. gregaria</i> (Donkin)	0.00	0.00	2.28
<i>N. lanceolata</i> (Agardh) Kütz.	0.00	0.82	2.43
<i>N. minuscula</i> Grunow	0.00	0.35	0.51
<i>N. viridula</i> (Kütz.) Ehrenb.	0.00	0.00	0.30
<i>Nitzschia acicularis</i> (Kütz.) W. Sm.	0.00	0.00	4.25
<i>N. amphibia</i> Grunow	0.00	3.11	0.92
<i>N. capitellata</i> Hust.	8.46	3.17	0.31
<i>N. clausii</i> Grunow	0.00	1.07	0.10
<i>N. constricta</i> (Kütz.) Grunow	0.00	0.00	0.52
<i>N. dissipata</i> (Kütz.) Grunow	0.00	0.66	3.35
<i>N. fonticola</i> Grunow	0.00	0.00	0.38
<i>N. inconspicua</i> Grunow	0.00	3.96	1.49
<i>N. linearis</i> (Agardh) W. Sm.	0.00	0.79	1.96
<i>N. microcephala</i> Grunow	0.00	0.00	0.20
<i>N. nana</i> Grunow	0.00	0.82	0.18
<i>N. palea</i> (Kütz.) W. Sm.	0.00	1.33	1.81
<i>N. perminuta</i> (Grunow) M. Perag.	0.00	2.42	1.70
<i>N. recta</i> Hantzsch	0.00	0.35	0.41
<i>Pinnularia microstaurum</i> (Ehrenb.) W. Sm.	0.06	0.13	0.00
<i>P. obscura</i> Krasske	1.74	14.79	0.00
<i>P. subcapitata</i> W. Greg.	5.93	1.77	0.00
<i>Planorthis lanceolatum</i> (Bréb.) Round & Bukht.	0.00	0.84	2.84
<i>Reimeria sinuata</i> (Greg.) Kociolek & Stoermer	0.00	0.33	1.29
<i>Rhoicosphenia curvata</i> (Kütz.) Grunow	0.00	0.33	0.33
<i>Sclaphora pupula</i> (Kütz.) Mereschk.	0.00	0.21	0.10
<i>Surirella angusta</i> Kütz.	0.00	0.00	0.20
<i>S. brebissonii</i> Krammer & Lange-Bert.	0.00	0.49	2.40
<i>S. ovalis</i> Bréb.	0.00	0.20	0.21
<i>Synedra delicatissima</i> W. Sm.	0.00	0.16	0.53
<i>S. ulna</i> (Nitzsch) Ehrenb.	0.45	1.24	1.82

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Joseph T. Hannibal and Joe B. Keiper, Editors

INSTRUCTIONS FOR AUTHORS

Authors are invited to submit manuscripts on topics that are within The Cleveland Museum of Natural History's sphere of interest. These include manuscripts on: archaeology, botany, cultural and physical anthropology, conservation, ecology, evolution, geology, paleontology, systematics, and zoology. Specimen-based research, especially that based on Cleveland Museum of Natural History specimens, is most welcome. All manuscripts and correspondence regarding manuscripts should be directed to either Joseph T. Hannibal or Joe B. Keiper, co-editors of *Kirtlandia*, at: The Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, Ohio 44106-1796, USA (hannibal@cmnh.org, jkeiper@cmnh.org).

Submit three copies of the manuscript, double-spaced on 8.5 x 11.0 inch (21.5 x 28 cm), or similar sized, paper, with only one space after each period. Abstracts should be concise and convey the main points and conclusions of the paper. Main headings should be centered and bold. Headings, as well as citations in text and in the references, should follow the style used in the most recent issue of the journal. Long tables should be submitted as appendices.

Citations should be cited in text as follows: Krebs (1994) or (Krebs, 1994); Krebs et al. (2002) or (Krebs et al., 2002); Teraguchi and Lublin (1999) or (Teraguchi and Lublin, 1999). If specific details from a book or article are cited, or if material is quoted or paraphrased, provide page citations as in these examples: (Miller, 1989, p. 261), or Teraguchi and Lublin (1995, p. 4–5). References should be cited in the text in chronological order, e.g.: Krebs, 1994; Teraguchi and Lublin, 1999; Krebs et al., 2002.

Tables should be concise and convey information not repeated in text. Use tabs in the word processor to create tables. Do not use spread-sheets such as Excel or Access or databases to create tables. Figures are to be black and white, and high quality, meaning 300 dpi for grayscale images (photographs) and 600 dpi for bitmap lineart (maps, illustrations, etc.). High quality TIF images submitted electronically can be used with approval by the editors. All figures are to be numbered sequentially and referenced in the text (e.g., Figure 1, Figure 2, etc.). Subfigures are indicated alphabetically, and labeled as A, B, C, etc. Figure legends should be written following the style below (example refers to a two-part figure):

Figure 1. Tubercled blossom, *Epioblasma torulosa torulosa* (Rafinesque, 1820), currently extirpated from Ohio; A, shell exterior; B, shell interior. Scale bar equals 1 cm.

Italicize genus and species names, and give species authority and year of description when species are first mentioned in the text. If a long table or appendix of taxa is presented, authorities and years may be excluded from the text but must be reported in the table. For papers dealing with systematics, give the original reference describing the taxa presented. Unless a large number of taxa are noted, list the works naming species in the references at the end of your manuscript.

Instructions on preparation of the final copy of the manuscript will be provided upon acceptance. Page charges and reprint charges will be determined by the editors. The final software for the final submission of a paper must be on a PC-compatible CD in WordPerfect 12.0 or previous versions, or MS-Word from MS Office 2003 or previous versions.

References

- Krebs, C. J. 1994. Ecology: The Experimental Analysis of Distribution and Abundance. Fourth Edition. Harper Collins, New York. 801 p.
- Krebs, R. A., H. M. Griffith, and M. J. S. Tevesz. 2002. A study of the Unionidae of Tinkers Creek, Ohio. *Kirtlandia*, 53:9–25.
- Miller, B. B. 1989. Screen-washing unconsolidated sediments for small macrofossils, p. 260–263. In R. M. Feldmann, R. E. Chapman, and J. T. Hannibal (eds.), *Paleotechniques*. Paleontological Society Special Publication, No. 4.
- Teraguchi, S. E., and K. J. Lublin. 1999. Checklist of the moths of Pallister State Nature Preserve, Ashtabula County, Ohio (1988–1992) with analyses of abundance. *Kirtlandia*, 51:3–18.

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